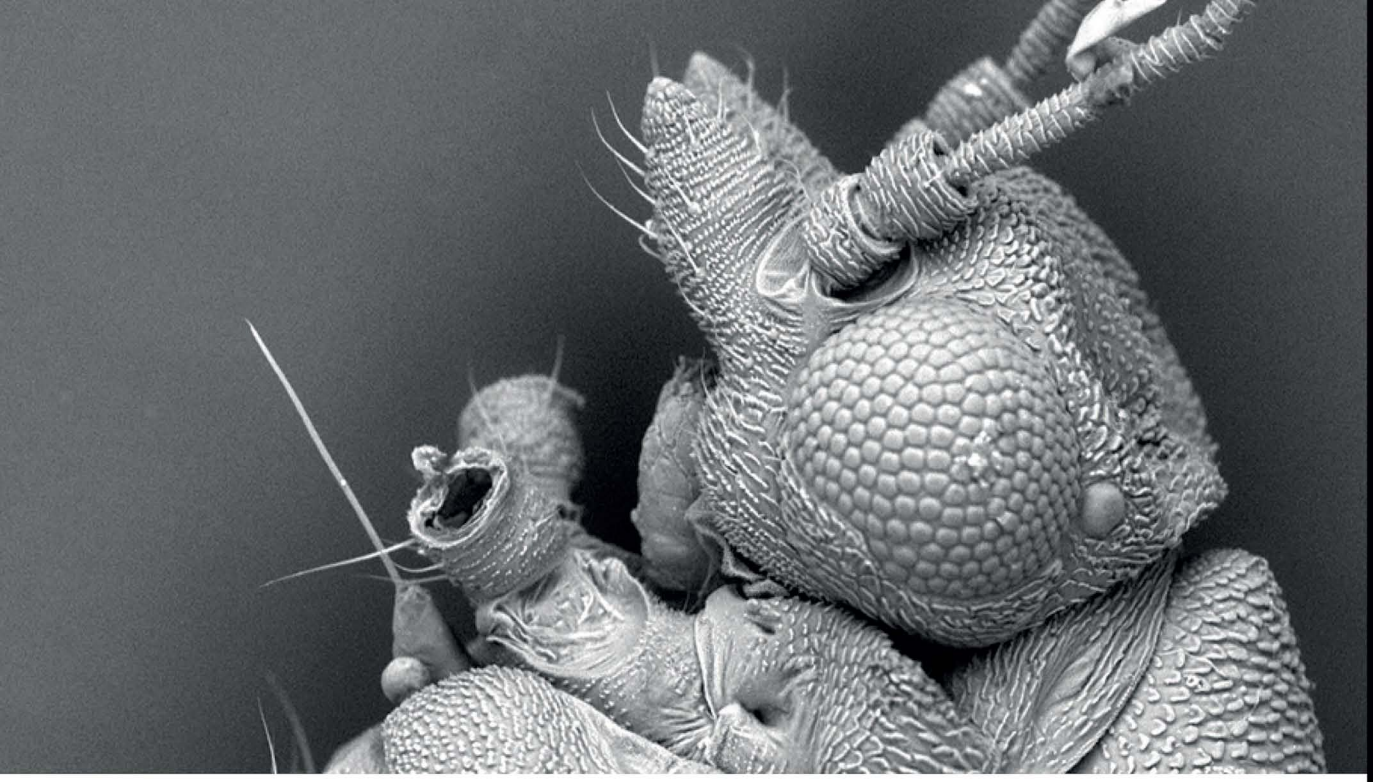


Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)

Jowita Drohojowska

WYDAWNICTWO
UNIWERSYTETU ŚLĄSKIEGO
KATOWICE 2015

Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)

NR 3414

Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)

Jowita Drohojowska

Wydawnictwo Uniwersytetu Śląskiego • Katowice 2015

Editor of the series: Biologia
Iwona Szarejko

Referee
Jacek Szwedo

Contents

Abstract

The paper presents the description and documentation of the thorax structure in 59 species of psyllids – representatives of all families and subfamilies (with the exception of Atmetocraniinae, Metapsyllinae and Symphorosinae) within the Psylloidea superfamily in accordance with the classification introduced by Burckhardt and Ouvrard (2012). The paper also provides structural characteristics of that part of body in the Liadopsyllidae fossil family regarded as the ancestors of modern psyllids and the Aleyrodoidea insects, a group regarded as a sister group within the Sternorrhyncha suborder. Both groups have been applied as outgroups.

Based on the paleontological criterion as well as comparisons within and outside of groups, an analysis has been conducted regarding the directions of changes of the elements of thorax structures including the appendages. The polarization of characters has also been determined. The determination of phylogenetic relations based on the morphology of the thorax and its appendages has been conducted by means of cladistic analysis. The relations between the analyzed taxa have been presented in cladograms. The phylogenetic relations between the taxa of psyllids have been reviewed based on the analysis of the thorax including the appendages in comparison with other proposals of this group's phylogeny. The monophyly of five families has been confirmed: Carsidaridae, Homotomidae, Psyllidae, Phacopteronidae and Triozidae. In the structure of the thorax and the appendages, no synapomorphy confirming the monophyly of the following families has been established: Aphalaridae, Calophyidae and Liviidae. The characteristics of families and subfamilies have been complemented with new characters identified within the thorax. Based on the above, a key has been created for the identification of psyllids from individual subfamilies of the world fauna of psyllids.

Keywords: morphology, thorax, Hemiptera, Sternorrhyncha, Psylloidea

Acknowledgements

I owe a debt of gratitude to the late Professor Sędzimir Maciej Klimaszewski for his inspiration and encouragement in my pursuit of the study of psyllids.

My special gratitude is due to Professor Daniel Burckhardt (Naturhistorisches Museum Basel, Switzerland) for his generous assistance and lending of specimens.

I would also like to express my thanks to: Professor Pavel Lauterer (Moravian Museum, Brno, Czech Republic); Dr Igor Malenovsky (Moravian Museum, Brno, Czech Republik); Dr Evgenia Labina (Russian Academy of Sciences, Sankt Petersburg, Russia); Professor Li Fasheng (China Agricultural University, Beijing, China); Dr Luo Xinyu (China Agricultural University, Beijing, China) and Dr Cheryl Barr (Essig Museum of Entomology, University of California, Berkeley, California, USA) for the loan of psyllid specimens.

I am indebted to Professor Aleksander Herczek, Professor Wacław Wojciechowski and Professor Piotr Węgierek (Department of Zoology, University of Silesia, Katowice) for their valuable comments during the preparation of the manuscript.

I thank Dr Dagmara Żyła (Natural History Museum of Denmark / University of Copenhagen, Denmark) for her help in preparing the cladograms.

I would also like to thank Dr Magdalena Kowalewska (Scanning Microscopy Laboratory of the Museum and Institute of Zoology, Polish Academy of Science, Warsaw) and Adrian Mościcki, M.Sc.Eng. (Scanning Microscopy Laboratory of the Silesian University of Technology, Gliwice) for taking the SEM photographs. Special thanks go to Dr Jagna Karcz (Scanning Microscopy Laboratory of the Faculty of Biology and Environmental Protection of the University of Silesia) and to the staff of the Scanning Microscopy Laboratory of the Jagiellonian University in Cracow for the preparation of insects for analyses using the SEM microscope.

I would like to thank Marzena Zmarzły, MA (Department of Zoology, University of Silesia, Katowice) for the preparation of drawings.

I thank my colleagues from the Department of Zoology, University of Silesia, for their kind cooperation and assistance, especially Dr Ewa Simon and Dr Małgorzata Kalandyk-Kołodziejczyk, who encouraged me to perform this research.

Introduction

The morphological studies regarding insects from the Psylloidea superfamily conducted up to now focused mostly on the morphology of the head, forewings, legs and genitalia. In comparison to their total body dimensions, the thorax of psyllids is relatively large, yet not much information concerning its morphology is given in professional literature. It may thus be considered the least studied body part of these insects. Most information pertains to characters of diagnostic significance, and little characters of that kind have been found in the morphology of the thorax so far. It should not also be neglected that the thorax is a truly complex tagma of the body, which is difficult to mount. No studies of thorax in representatives of all higher taxonomic units have been conducted up to now (families, subfamilies or tribes of psyllids). Neither has any set of characters of the thorax which could serve as a determinant of affiliation of a given species to these units been distinguished. What is more, the morphological characters of the thorax have not been used in phylogenetic discussions regarding the Psylloidea. It has thus been decided to conduct a morphological analysis of the thorax in all families, subfamilies and tribes as well as to determine the feasibility of the distinguished characters for the determination of phylogenetic relations within the Psylloidea superfamily.

Review of previous studies of thorax morphology of psyllids

Audouin (1824) was the author of the first work regarding thorax morphology in insects. In his work, Audouin proposed a nomenclature for individual sclerites of the thorax of all orders of insects, as well as developed a topological definition for each of the sclerites constituting the thorax. Many of the contemporarily used terms relating to morphological structures and the thorax, such as episternum or trochantin, are derived from that particular work.

The first information regarding the structure of the thorax of psyllids have been provided by Witlaczil (1885), who studied the structures of the thorax in *Psyllopsis fraxinicola* (Foerster, 1848). That work, however, concerned mostly the anatomy of psyllids, so the information regarding the thorax was scarce and mostly related to the segmentation of the thorax into prothorax, mesothorax and metathorax.

In his works, Snodgrass (1908, 1909) has provided descriptions of numerous structures and has introduced names for individual structures of the thorax in insects, which are commonly used until present, also in the Psylloidea group. He has characterized and presented the drawings of the parapteron (Lat. *parapterum*), the peritreme (Lat. *peritrema*), the pleural sulcus (Lat. *sutura pleuralis*), the pleural wing process (Lat. *processus anterior alae*) and the preepisternum (Lat. *proepisternum*).

The thorax of psyllids was described in detail by Stough (1910) in his work regarding the species *Pachypsylla celtidismamma* (Fletcher, 1883). Based on Audoin's (1824) work referred to above, Stough (1910) has characterized the individual tagmata of the psyllids' thorax by describing and drawing all the constituent sclerites. While Stough (1910) has only provided information regarding a single species, the subsequent work written by Crawford (1914) has reviewed 7 species of different genera of New World psyllids. The author attempted to indicate homology between the individual elements of the thorax and to interpret their function and origin. He has given special attention to the three additional sclerites between the prothorax and mesothorax, the incompletely developed mesopleural sulcus, the meso- and metasternum, as well as the metapleurae. At the same time, he disagreed with the interpretation of sclerites proposed by Stoug (1910) and has complemented his descriptions with structures which were not included earlier. Moreover, he has illustrated the internal structure of the thorax of psyllids. In that same year, a series of works by Crampton (1914a, b, c) was published, in which the author has discussed the structure of the thorax of winged insects, at the same time introducing a number of morphological terms applied in descriptions of insects including psyllids until present.

Taylor (1918), while studying the *Euglyptoneura robusta* (Crawford, 1914) and *Apsylla cistellata* (Buckton, 1896) species, attempted to reinterpret the illustrations, notions and conclusions drawn from the structure of the psyllids' thorax by Crawford (1914) while resorting to the works of Crampton, referred to above. In the work, the author has also included conclusions regarding the thorax morphology of 8 contemporarily distinguished families within the Homoptera suborder and 17 families within the Heteroptera suborder. Based on these conclusions, he has developed a general structural plan of Heteroptera and Homoptera. He has also proposed relationships within the Hemiptera order based on the thorax structure and provided proper schematic illustrations.

Subsequent researchers such as Brittain (1922) and Minkiewicz (1924), who based their research on the *Psylla mali* Schmidberger, 1836 or Bosselli (1928), studying the thorax morphology of the *Homotoma ficus* (Linnaeus, 1758), did not go beyond the scheme provided by Crawford (1914) in their works.

It was only Weber (1929) who described the *Psylla mali* head and thorax structure while providing a series of new data regarding that part of the body. Weber's monograph is an accurate study of *P. mali,* in which the author characterized the external and internal structures of the head and thorax and supplemented the detailed descriptions with excellent drawings. He presented the dimensions and shapes of individual sclerites and the occurring structures, as well as the courses of most muscles, their proximal and distal attachment points at the prothorax, mesothorax and metathorax apodemes. He was the first to indicate the trochantinal apodeme at the meso- and metathorax and the mode of attachment and course of the "pleurotrochantinal muscles" which make psyllids capable of jumping. His work included a comparison of the muscular system of individual sections of the thorax and the mechanics of the psyllids' muscles with other insects – both jumping (Auchenorrhyncha) and ones that lack this capability (Aphidoidea, Lepidoptera). Although it was published nearly a century ago, the drawings from this work are commonly copied by modern researchers, especially in descriptions of the psyllids' muscular system.

Pflugfelder (1941) published a monograph of insects classified in the contemporary Psyllina suborder, in which he has presented the structure of the psyllids' thorax while quoting descriptions and reproducing drawings from the works of Crawford (1914) and Weber (1929). This work also included a systematic part, in which the author provided the morphological characteristics of species classified in all 7 contemporarily distinguished subfamilies of the Psylloidea family from the Psyllina suborder. In case of species from 4 subfamilies (Liviinae Löw, Aphalarinae Löw, Psyllinae Löw and Triozinae Löw), the

author pointed out a differing shape of the pronotum in each subfamily as a defining character.

A unique approach towards the analyses of psyllids' thorax morphology was presented by Heslop-Harrison (1951), who was looking for morphological characters of adult specimens that would be useful for creating a natural taxonomic system of the Psylloidea. Within the thorax, he has only found such characters in the prothorax, while regarding the remaining two tagmas – the mesothorax and metathorax – as devoid of such characters. The author analyzed the episternal sclerites and has noted the number and distribution of stigmas at the peritremes.

In the introduction regarding morphology in his monograph of psyllids fauna of contemporary Czechoslovakia, Vondraček (1957) provided a graphical presentation of the dorsal and lateral *Arytaina genistae* (Latreille, 1804) tagma of a species that has not been studied before, in the form of general drawings devoid of several significant morphological elements such as the pleural sulci (Lat. *sutura pro-*, *meso-*, *metapluralis)*, the additional sclerites (Lat. *scleritum accessorium*) or the metathorax pleurites (*metaepimerum, metaepisternum)*.

In his work regarding the taxonomic system of the contemporary Psyllodea infraorder, Klimaszewski (1964) analyzed the structure of the thorax for the purposes of comparing higher taxonomic units – families. The author analyzed the morphology of 13 species of psyllids and proved that the relations between the pronotum, mesopraescutum and mesoscutum may be used for inferring lineages and relations between species from individual families. He pointed out the wide pronotum and relatively even development of the mesopraescutum and mesoscutum as plesiomorphic characters and undermined the common opinion that the development of the meracanthus is an apomorphic character. The author based his conclusions mostly on his own research, including his own descriptions and drawings, and on the data of two species described in the literature (Crawford 1914, Weber 1929). It was the first comparative analysis of thorax morphology of psyllids classified in individual families distributed all over the world, whereas Crawford (1914) only based his work on Nearctic material.

Also the work by Tremblay (1965) is significant in the view of studying the thorax of psyllids. The author was the first to describe the *Trioza tremblayi* Wagner, 1961 and to adapt the nomenclature concerning the morphology of the thorax of insects provided earlier by Snodgrass (1908, 1909, 1927, 1935). It was the first time that Snodgrass' terminology was applied in describing psyllids.

Apart from describing the morphology of the thorax of insects classified in 30 orders, Matsuda (1970) also discussed the probable evolution of individual elements of the thorax, homologies between its respective parts and the main evolutionary changes in the muscular system of imago and nymphs. He also introduced new morphological terms used up to now, such as the anapleural cleft (Lac. *sutura anapleuralis*), that is the cleft dividing the pleura into the dorsal and ventral parts. For that purpose the author used the drawings of tergites and pleurites from the work by Weber (1929).

Based on the nomenclature provided by Matsuda, Journet and Vickery (1978) conducted a study of the morphology of adult insects and Nearctic larvae of species classified as *Craspedolepta* Enderlein, 1921. They presented their own drawings of individual elements of the segments in concern, which has contributed to the general knowledge of their morphology.

Further developments in discovering the thorax structure were due to the works by Hodkinson and White (1979), Brown and Hodkinson (1988), Ossiannilsson (1992). In the introductions to their works, the authors discussed the morphological structure of psyllids, thus standardizing the terminology used in describing psyllids. In all works referred to above, however, the authors neglected the ventral side.

In their work, Ouvrard et al. (2002) described the structure of the pleuron in 7 species from 3 selected families – with consideration given to both internal and external sides. The authors pointed out the elements of the thorax which are characteristic only to psyllids, such as the transepimeral sulcus in the mesothorax, the

fossa of the trochantinal apodeme or the anapisternal disc. They also described the probable manners of shifting and forming of the pleuron elements, especially in the metathorax. What is more, they compared all the morphological terms used earlier by various authors. In their work regarding the wing base articulation (Ouvrard et al., 2008), the authors have characterized and illustrated all the elements and structures allowing for the movement of wings in psyllids, as well as presented the dorsal thorax sclerites.

In recent years, Drohojowska has taken up studies of variation in the morphology of the thorax of psyllids. The results of the studies have been published in three works (Drohojowska 2009a, b, 2013). For the first time, the thorax of male and female specimens has been compared (8 species from various families and genera) and it became clear that the shape and proportions of individual thorax pleura are similar and the differences only concern sizes (Drohojowska, 2009b). In her work of 2013, the author has studied the thorax of species of the *Cacopsylla* Ossiannilsson, 1970 genus classified as three subgenera, and indicated the characters which may be used in their diagnostics.

In the introduction to his monograph containing descriptions and redescriptions of over 3.500 species of psyllids of China, Li (2011) has provided a description of the thorax based on the *Cacopsylla chinensis* Yang, Li, 1981 species. Despite the great number of analyzed species, the author did not include the description or drawings of the dorsal and ventral sides of the thorax.

In the papers based on fossil material, where the Psylloidea superfamily is relatively well represented, there is little information regarding the thorax of psyllids. Except for Klimaszewski (1997), Ouvrard et al. (2010) and Drohojowska (2011), no descriptions of the thorax part may be found. Similarly, little information is provided in the works regarding the modern fauna of psyllids. While, as far as the fossil material is concerned, the above may be understood due to the preservation condition of specimens, it should not cause difficulties in case of modern material.

1 Material and methods

The analysis was based on imago forms of 73 species of psyllids and encompassed the making of 2.500 figures of the morphological structures of the thorax using a SEM microscope. 59 species, of which high-quality photographs were taken, were selected for the description of thorax morphology and phylogeny of Psylloidea (Table 1). The species were selected in such a way as to represent all families, subfamilies and tribes currently distinguished in the Psylloidea superfamily in accordance with the Burckhardt, Ouvrard (2012) classification with further alterations (Burckhardt, Queiroz 2013). No material from three monotype subfamilies (Atmetocraniinae, Metapsyllinae, Symphorosinae) classified as members of the Calophydiae family and two monotype tribes (Diceraopsyllini and Synozini) from the Homotomidae family was obtained. The analysis was based on both unpublished data and results that had already been published by the author.

Adult psyllids were collected with an entomological sweep-net and killed in vapours of potassium cyanide. After removing the wings and legs, the specimens were mounted on a stub for the analysis in a low vacuum electron scanning microscope. Dried insects on inspect pins had their wings and legs removed and were subsequently taken off the pins and stuck directly to an aluminium table using carbon tape or were stuck to a glass plate and then to the aluminium table. In cases when the insects were kept as wet collections, stored in alcohol, before removing the appendices and sticking to the table they had to undergo preservation processes using 3% phosphate buffered glutaraldehyde, rinsing with phosphate buffer and dehydration in alcohol series. The specimens were subsequently dried in CPD (Critical Point Drying). All procedures for the preparation of insects for analyses using a SEM microscope were conducted in the Department of Zoology, Scanning Microscopy Laboratory of the Faculty of Biology and Environmental Protection of the University of Silesia and the Scanning Microscopy Laboratory of the Jagiellonian University in Cracow. The insects did not undergo ultrasonic washing as the specimens were damaged that way. The insects also weren not sputter-coated with gold (this would make the photographical documentation impossible using the proposed methods). Using a scanning microscope, each specimen was analyzed from the dorsal, ventral and side planes. To achieve that, Hitachi S-3400N scanning electron microscopes of the Scanning Microscopy Laboratory at the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, and Scanning Microscopy Laboratory at the Silesian University of Technology's Institute of Materials Science of the Faculty of Materials Engineering and Metallurgy of the Silesian University of Technology in Gliwice were used. Prior to the analysis using the scanning microscope, the insects were analyzed using a Nikon MZ1500 stereoscopic microscope. Corel Photo-Paint X5 software was used for the graphical editing of diagrams and photographs.

The cladistic analysis was conducted using the following methods and assumptions:

Table 1. The list of the psyllids that were analyzed (classification according to Burckhardt and Ouvrard 2012 altered by Burckhardt and Queiroz 2013). Taxa listed in alphabetical order

Family	Subfamily	Tribe	Species
1	2	3	4
Aphalaridae Löw, 1879	Aphalarinae Löw, 1879		*Aphalara polygoni* Foerster, 1848; Fig. 5 *Caillardia robusta* Loginova, 1956; Figs. 6, 64 *Colposcenia jakowleffi* (Scott, 1879); Fig. 7 *Craspedolepta sonchi* (Foerster, 1848); Fig. 8 *Gyropsylla spegazziniana* (Lizer, 1919); Fig. 9 *Xenaphalara signata* (Löw, 1881); Fig. 10
	Pachypsyllinae Crawford, 1914		*Pachypsylla venusta* (Osten-Sacken, 1861); Fig. 11
	Rhinocolinae Vondraček, 1957		*Agonoscena pistaciae* Burckhardt, Lauterer, 1989; Fig. 12 *Apsylla cistellata* (Buckton, 1896); Fig. 13 *Rhinocola aceris* (Linnaeus, 1758); Fig. 14
	Spondyliaspidinae Schwarz, 1898		*Blastopsylla occidentalis* Taylor, 1985; Figs. 15, 65 *Creiis tecta* Maskell, 1898; Fig. 16 *Glycaspis brimblecombei* Moore, 1964; Fig. 17
	Togepsyllinae Becker-Migdisova, 1973		*Togepsylla matsumurana* Kuwayama, 1949; Fig. 18
Calophyidae Vondraček, 1957	Atmetocraniinae Becker-Migdisova, 1973		—
	Calophyinae Vondraček, 1957		*Calophya rhois* (Löw, 1877); Fig. 19
	Mastigimatinae Becker-Migdisova, 1973		*Bharatiana octospinosa* Mathur, 1973; Fig. 20 *Cecidopsylla schimae* Kieffer, 1905; Fig. 21 *Mastigimas reseri* Burckhardt, Queiroz and Drohojowska, 2013; Fig. 22
	Metapsyllinae Kwon, 1983		—
	Symphorosinae Li, 2002		—
Carsidaridae Crawford, 1911			*Mesohomotoma lineaticollis* Enderlein, 1914; Fig. 23 *Tenaphalara acutipennis* Kuwayama, 1908; Fig. 24
Homotomidae Heslop-Harrison, 1958	Dynopsyllinae Becker-Migdisova, 1973	Diceraopsyllini Hollis and Broomfield, 1989	—
		Dynopsyllini Becker-Migdisova, 1973	*Triozamia lamborni* (Newstead, 1914); Fig. 25
	Homotominae Heslop-Harrison, 1958	Homotomini Heslop-Harrison, 1958	*Homotoma ficus* (Linnaeus, 1758); Fig. 26
		Synozini Becker-Migdisova, 1973	—
	Macrohomotominae White and Hodkinson, 1985	Edenini Bhanotar, Ghosh and Ghosh, 1972	*Mycopsylla fici* (Tryon, 1895); Fig. 27

cont. tab. 1

1	2	3	4
		Macrohomotomini White and Hodkinson, 1985	*Macrohomotoma gladiata* Kuwayama, 1908; Fig. 28
		Phytolymini White and Hodkinson, 1985	*Phytolyma fusca* Alibert, 1947; Fig. 29
Liviidae Löw, 1879	Euphyllurinae Crawford, 1914	Diaphorinini Vondraček, 1951	*Diaphorina truncata* Crawford, 1924; Fig. 30 *Psyllopsis fraxinicola* (Foerster, 1848); Fig. 31
		Euphyllurini Crawford, 1914	*Euphyllura olivina* (Costa, 1839); Fig. 32
		Pachypsylloidini Loginova, 1964	*Pachypsylloides reverendus* Loginova, 1970; Fig. 33
		Strophingiini White and Hodkinson, 1985	*Strophingia cinereae* Hodkinson, 1971; Fig. 34 *Strophingia proxima* Hodkinson, 1981; Fig. 35
	Liviinae Löw, 1879		*Camaratoscena speciosa* (Flor, 1861); Fig. 36 *Livia junci* (Schrank, 1798); Fig. 37 *Paurocephala psylloptera* Crawford, 1913; Fig. 38 *Syntomoza unicolor* (Loginova, 1958); Fig. 39
Phacopteronidae Heslop-Harrison, 1958			*Pseudophacopteron zimmermanni* (Aulmann, 1912); Figs. 40, 66
Psyllidae Latreille, 1807	Acizziinae White and Hodkinson, 1985		*Acizzia hollisi* Burckhardt, 1981; Fig. 41
	Aphalaroidinae Vondraček, 1963		*Russelliana solanicola* Tuthill, 1959; Fig. 42
	Ciriacreminae Enderlein, 1910		*Auchmerina tuthilli* Klimaszewski, 1962; Fig. 43 *Ciriacremum nigripes* Hollis, 1976; Fig. 44 *Heteropsylla cubana* Crawford, 1914; Fig. 45
	Macrocorsinae Vondraček, 1963		*Euphalerus vittatus* Crawford, 1912; Fig. 46
	Psyllinae Latreille, 1807		*Anomoneura mori* Schwarz, 1896; Fig. 47 *Arytaina maculata* (Löw, 1886); Fig. 48 *Cacopsylla ambiqua* (Foerster, 1848); Fig. 49 *Cacopsylla crataegi* (Schrank, 1801); Fig. 50 *Cacopsylla peregrina* (Foerster, 1848); Fig. 51 *Cyamophila bajevae* Loginova, 1978; Fig. 52 *Psylla foersteri* Flor, 1861; Fig. 53 *Psylla fusca* Zetterstedt, 1828; Fig. 54
Triozidae Löw, 1879			*Bactericera bielawskii* (Klimaszewski, 1963); Fig 55 *Bactericera curvatinervis* (Foerster, 1848); Fig. 56 *Calinda pehuenche* Olivares and Burckhardt, 1997; Fig. 57 *Egeirotrioza ceardi* (Bergevin,1926); Fig. 58 *Trichochermes walkeri* (Foerster, 1848); Fig. 59 *Trioza anthrisci* Burckhardt, 1986; Fig. 60 *Trioza berberidis* Burckhardt, 1988; Fig. 61 *Trioza galii* Foerster, 1848; Fig. 62 *Trioza malloticola* (Crawford, 1928); Fig. 63

Maximum parsimony (MP) was used as a phylogenetic method. The character matrix was created using Mesquite ver. 2.71 (Maddison, Maddison 2011). The character list begun with character 1. The matrix included 82 characters (numbered 1–82) scored for 61 taxa. Unknown character states were marked with "?". The analyses were designed in TNT 1.1 software (Goloboff et al., 2008) using the "Traditional Search" algorithm to find the most parsimonious trees. The following parameters were used: "memory set – 10.000 trees"; "tree bisection–reconnection (TBR) branch-swapping algorithm" with "10 replications," "saving 100 trees per replicate" and "zero-length branches collapse after the search." The consensus tree was calculated using the "majority rule consensus" method with a cut-off threshold of 50%. All character states were treated as unordered and equally weighted. Trees and features were studied using WinClada ver. 1.00.08 (Nixon 2002), and the subsequent graphical processing was conducted using Adobe® Photoshop CS6 and Adobe® Illustrator CS6 software.

The material for the purposes of the analysis was partially collected by the author in the area of Poland in the years 2003–2011. It has mostly been borrowed from the following entomological collections: Department of Zoology, University of Silesia, Katowice, Poland; Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; Naturhistorisches Museum Basel, Switzerland; Department of Entomology, Moravian Museum, Brno, Czech Republic; ESSIG Museum of Entomology, University of California, Berkeley, California, USA; Zoological Institute, Russian Academy of Sciences, Sankt Petersburg, Russia; Department of Entomology, China Agricultural University, Beijing, China. Consents to process the borrowed samples were obtained from all the institutions.

In the work, abbreviations were used for all morphological terms, mostly quoted after Ouvrard et al. (2002, 2008). All applied abbreviations have been presented in Table 2.

The measurements of individual thorax elements were acquired based on SEM photographs. The method of measuring the individual pleura

Table 2. Morphological terminology and the list of abbreviations used to describe the photographs, after Ouvrard et al. (2002, 2008) (see Figs 1–4)

Arranged alphabetically	For particular tagmata
1	2
aas – anterior accessory sclerite; Lat. *scleritum accessorium anterior*	PROTHORAX
acl2 – anapleural cleft; Lat. *sutura anapleuralis*	ccx1 – condyle of the procoxa
aem – anepimeron; Lat. *anepimerum*	cx1 – procoxa
aeps – anepisternum; Lat. *anepisternum*	epm1 – proepimeron
apwp – anterior pleural wing process; Lat. *processus anterior alae*	eps1 – proepisternum
axc2 – axillary cord on mesothorax; Lat. *frenulum squamulare mesothoracis*	li – labium
axc3 – axillary cord on metathorax; Lat. *frenulum squamulare metathoracis*	nt1 – pronotum
bas – basalare; Lat. *basalare*	pls1 – propleural sulcus
ccx1 – condyle of the procoxa; Lat. *condylus procoxalis*	st1 – prosternum
ccx2 – condyle of the mesocoxa; Lat. *condylus mesocoxalis*	
ccx3 – condyle of the metacoxa; Lat. *condylus metacoxalis*	MESOTHORAX
cx1 – procoxa; Lat. *procoxa*	aas – anterior accessory sclerite
cx2 – mesocoxa; Lat. *mesocoxa*	acl2 – anapleural cleft
cx3 – metacoxa; Lat. *metacoxa*	aem – anapimeron
epm1 – proepimeron; Lat. *proepimerum*	aeps – anapisternum
epm2 – mesepimeron; Lat. *mesoepimerum*	apwp – anterior pleural wing process
epm3 – metepimeron; Lat. *metaepimerum*	axc2 – axillary cord on mesothorax
eps1 – proepisternum; Lat. *proepisternum*	bas – basalare
eps2 – mesepisternum; Lat. *mesoepisternum*	ccx2 – condyle of the mesocoxa
eps3 – metepisternum; Lat. *metaepisternum*	cx2 – mesocoxa
fpa2 – fossa of the mesopleural apophysis; Lat. *fossa mesopleuralis apophysis*	epm2 – mesepimeron
fpa3 – fossa of the metapleural apophysis; Lat. *fossa metapleuralis apophysis*	eps2 – mesepisternum

cont. tab. 2

1	2
ftna2 – fossa of the mesothorax trochantinal apodeme; Lat. *fossa apodemae trochantinalis mesothoracis* ftna3 – fossa of the metathorax trochantinal apodeme; Lat. *fossa apodemae trochantinalis metathoracis* hepm – heel of the epimeron; Lat. *calx epimeri* kcx – katepisternal complex; Lat. *complexus katepisternalis* kem2 – katepimeron; Lat. *katepimerum* kes2 – katepisternum; Lat. *katepisternum* li – labium; Lat. *labium* mcs – meracanthus; Lat. *meracanthus* nt1 – pronotum; Lat. *pronotum* pas – posterior accessory sclerite; Lat. *scleritum accessorium posterior* pbr – prealar bridge; Lat. *praealare* peps – preepisternum; Lat. *praepisternum* pes – prescutoepisternal sulcus; Lat. *sutura prescutoepisternalis* pls1 – propleural sulcus; Lat. *sutura propleuralis* pls2 – mesopleural sulcus; Lat. *sutura mesopleuralis* pls3 – metapleural sulcus; Lat. *sutura metapleuralis* pnt2 – mesopostnotum; Lat. *mesopostnotum* pnt3 – metapostnotum; Lat. *metapostnotum* ppt – parapteron; Lat. *parapterum* psc2 – mesopraescutum; Lat. *mesopraescutum* pscs – posterior mesopraescutum suture; Lat. *sutura mesopraescuti posterior* pss – pleurosternal suture; Lat. *sutura pleurosternalis* ptm2 – mesothorax peritreme; Lat. *mesothoracis peritrema* ptm3 – metathorax peritreme; Lat. *metathoracis peritrema* pwp – posterior wing process; Lat. *processus posterior alae* sc2 – mesoscutum; Lat. *mesoscutum* sc3 – metascutum; Lat. *metascutum* scl2 – mesoscutellum; Lat. *mesoscutellum* scl3 – metascutellum; Lat. *metascutellum* scs – mesoscutum suture; Lat. *sutura mesoscuti* st1 – prosternum; Lat. *prosternum* st2 – basisternum; Lat. *basisternum* st3 – metasternum; Lat. *metasternum* stcx – sternocostal suture; Lat. *sutura sternocostalis* tems – transepimeral sulcus; Lat. *sulcus transepimeralis* tg – tegula; Lat. *tegula* trn2 – mesothorax trochantin; Lat. *trochantinus mesothoracis* trn3 – metathorax trochantin; Lat. *trochantinus metathoracis*	fpa2 – fossa of the mesopleural apophysis ftna2 – fossa of the mesothorax trochantinal apodeme hepm – heel of the epimeron kcx – katapisternal complex kem2 – katepimeron kes2 – katepisternum pas – posterior accessory sclerite pbr – prealar bridge peps – preepisternum pes – prescutoepisternal sulcus pls2 – mesopleural sulcus pnt2 – mesopostnotum ppt – parapteron psc2 – mesopraescutum pscs – posterior mesopraescutum suture pss – pleurosternal suture ptm2 – mesothorax peritreme st2 – basisternum sc2 – mesoscutum scl2 – mesoscutellum scs – mesoscutum suture stcx – sternocostal suture tems – transepimeral sulcus tg – tegula trn2 – mesothorax trochantin METATHORAX axc3 – axillary cord on metathorax ccx3 – condyle of the metacoxa cx3 – metacoxa epm3 – metepimeron eps3 – metepisternum fpa3 – fossa of the metapleural apophysis ftna3 – fossa of the metathorax trochantinal apodeme mcs – meracanthus pls3 – metapleural sulcus pnt3 – metapostnotum ptm3 – metathorax peritreme pwp – posterior wing process sc3 – metascutum scl3 – metascutellum trn3 – metathorax trochantin st3 – metasternum

and the boundaries between the pleura have been presented in Fig. 4. Explanation of abbreviations used in Fig. 4: **A** – pronotum width; **B** – pronotum length; **C** – mesopraescutum width; **D** – mesopraescutum length; **E** – mesoscutum width; **F** – mesoscutum length; **G** – length of anterio – lateral margin of the mesoscutum; **H** – length of posterior – lateral margin of the mesoscutum; **J** – mesoscutellum width; K – mesoscutellum length; **M** – metascutellum width; **N** – metascutellum length; **O** – anterior margin of the pronotum; **P** – posterior margin of the pronotum; **R** – anterior margin of the mesopraescutum; **S** – posterior margin of the meso-

praescutum, anterior margin of the mesoscutum; **T** – posterior margin of the mesoscutum, anterior margin of the mesoscutellum; **U** – posterior margin of the mesoscuetellum, anterior margin of the metascutum; **W** – posterior margin of the metascutum, anterior margin of the metascutellum; **Z** – posterior margin of the metascutellum, **WH** – head width always measured with eyes.

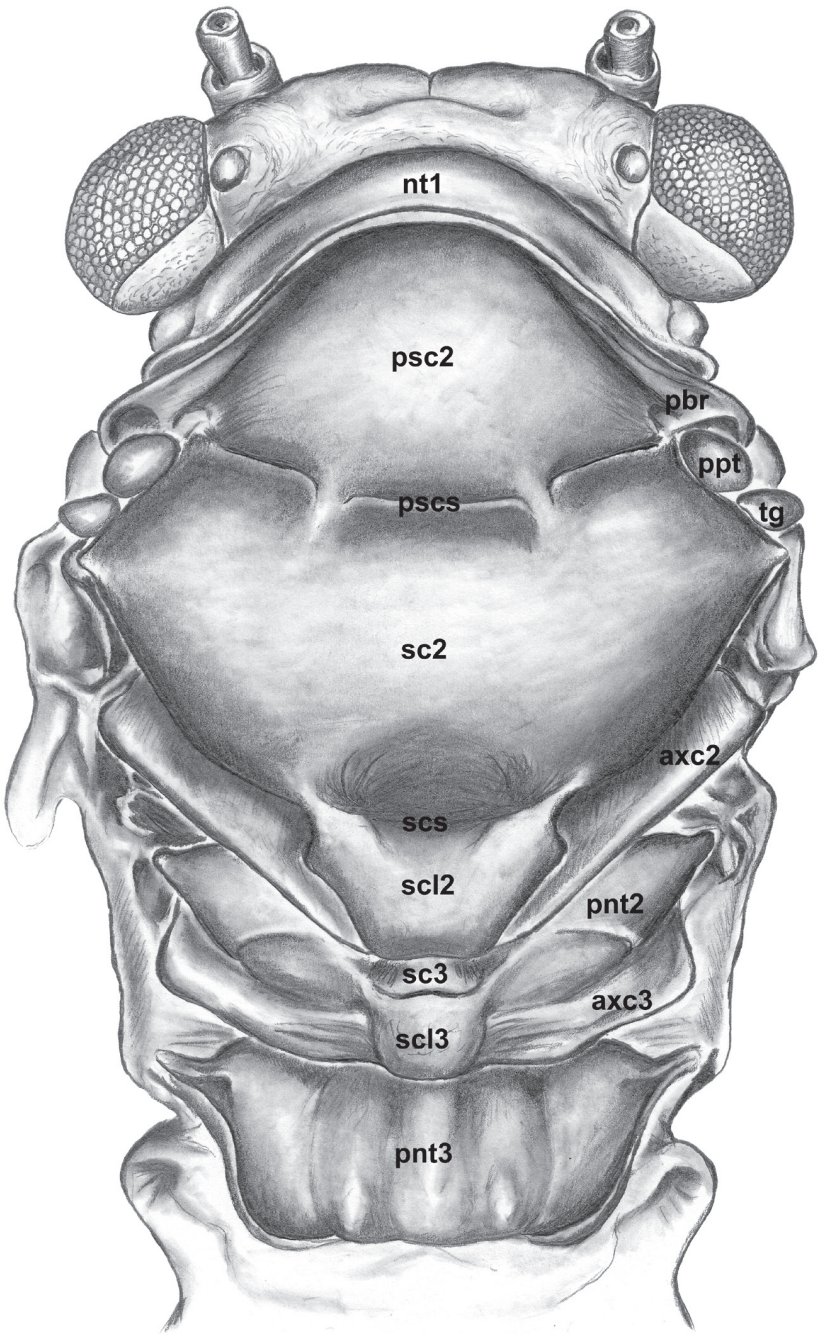


Fig. 1. Diagram of the dorsal view of thorax

Explanations: **axc2** – axillary cord on mesothorax; **axc3** – axillary cord on metathorax; **nt1** – pronotum; **pbr** – prealar bridge; **pnt2** – mesopostnotum; **pnt3** – metapostnotum; **ppt** – parapteron; **psc2** – mesopraescutum; **pscs** – posterior mesopraescutum suture; **sc2** – mesoscutum; **sc3** – metascutum; **scl2** – mesoscutellum; **scl3** – metascutellum; **scs** – mesoscutum suture; **tg** – tegula

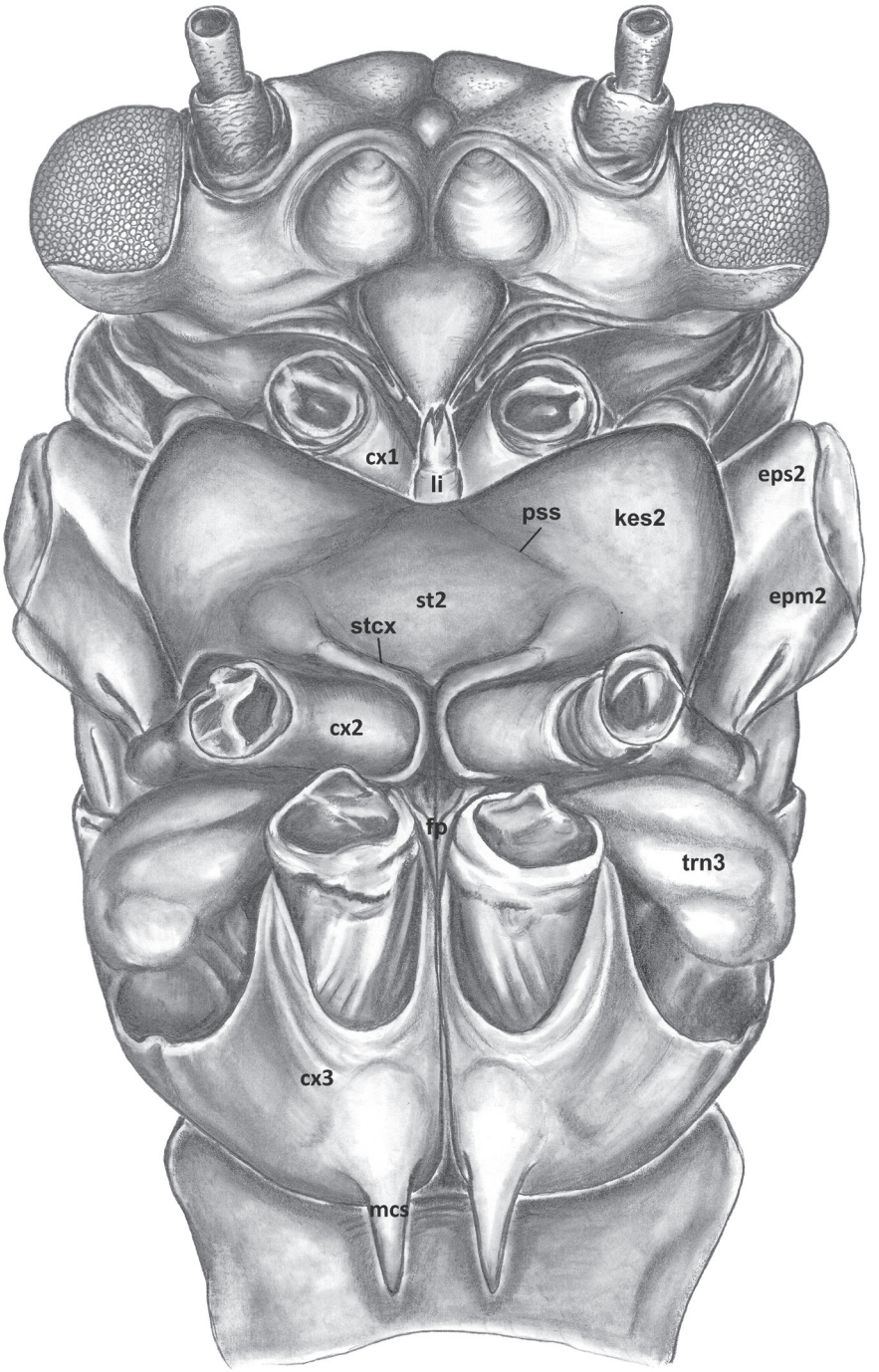


Fig. 2. Diagram of the ventral view of thorax

Explanations: **cx1** – procoxa; **cx2** – mesocoxa; **cx3** – metacoxa; **epm2** – mesepimeron; **eps2** – mesepisternum; **fp** – furcal pit on metathorax; **kes2** – katepisternum; **li** – labium; **mcs** – meracanthus; **pss** – pleurosternal suture; **st2** – basisternum; **stcx** – sternocostal suture; **trn3** – metathorax trochantin

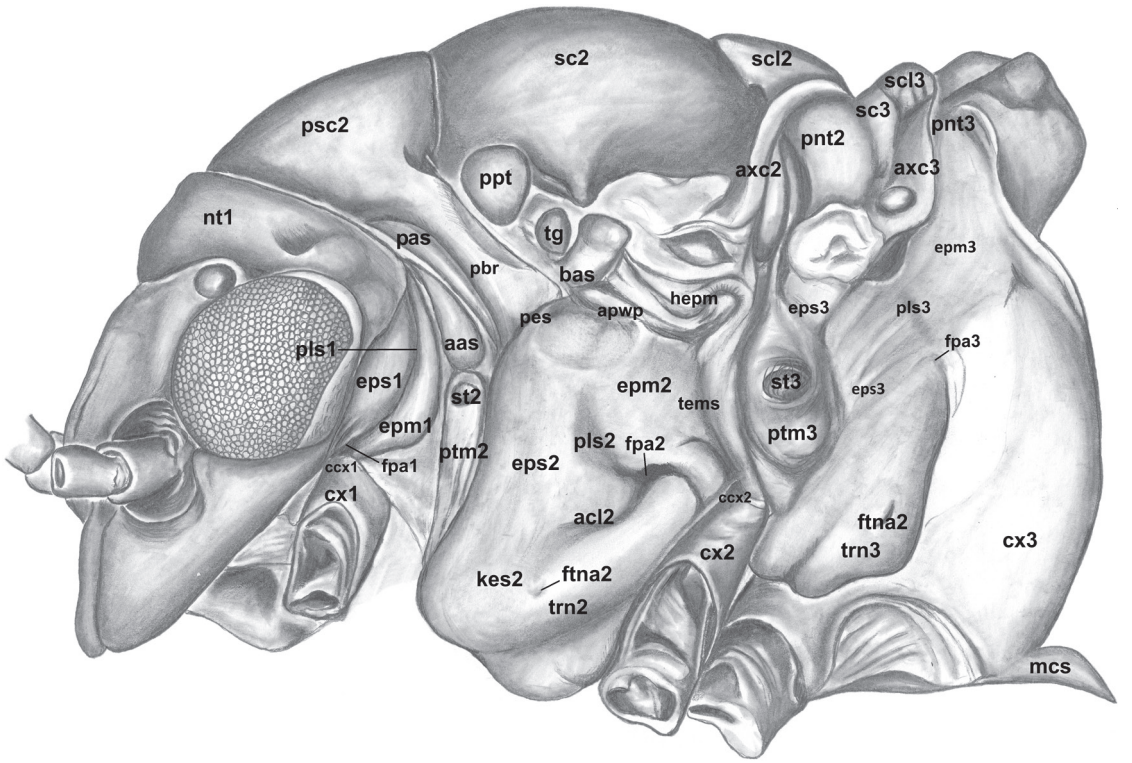


Fig. 3. Diagram of the lateral view of thorax

Explanations: **aas** – anterior accessory sclerite; **acl2** – anapleural cleft; **apwp** – anterior pleural wing process; **axc2** – axillary cord on mesothorax; **axc3** – axillary cord on metathorax; **bas** – basalare; **ccx1** – condyle of the procoxa; **ccx2** – condyle of the mesocoxa; **cx1** – procoxa; **cx2** – mesocoxa; **cx3** – metacoxa; **epm1** – proepimeron; **epm2** – mesepimeron; **epm3** – metepimeron; **eps1** – proepisternum; **eps2** – mesepisternum; **eps3** – metepisternum; **fpa2** – fossa of the mesopleural apophysis; **fpa3** – fossa of the metapleural apophysis; **ftna2** – fossa of the mesothorax trochantinal apodeme; **ftna3** – fossa of the metathorax trochantinal apodeme; **hepm** – heel of the epimeron; **kes2** – katepisternum; **mcs** – meracanthus; **nt1** – pronotum; **pas** – posterior accessory sclerite; **pbr** – prealar bridge; **pes** – prescutoepisternal sulcus; **pls1** – propleural sulcus; **pls2** – mesopleural sulcus; **pls3** – metapleural sulcus; **pnt2** – mesopostnotum; **pnt3** – metapostnotum; **ppt** – parapteron; **psc2** – mesopraescutum; **ptm2** – mesothorax peritreme; **ptm3** – metathorax peritreme; **sc2** – mesoscutum; **sc3** – metascutum; **scl2** – mesoscutellum; **scl3** – metascutellum; **tems** – transepimeral sulcus; **tg** – tegula; **trn2** – mesothorax trochantin; **trn3** – metathorax trochantin

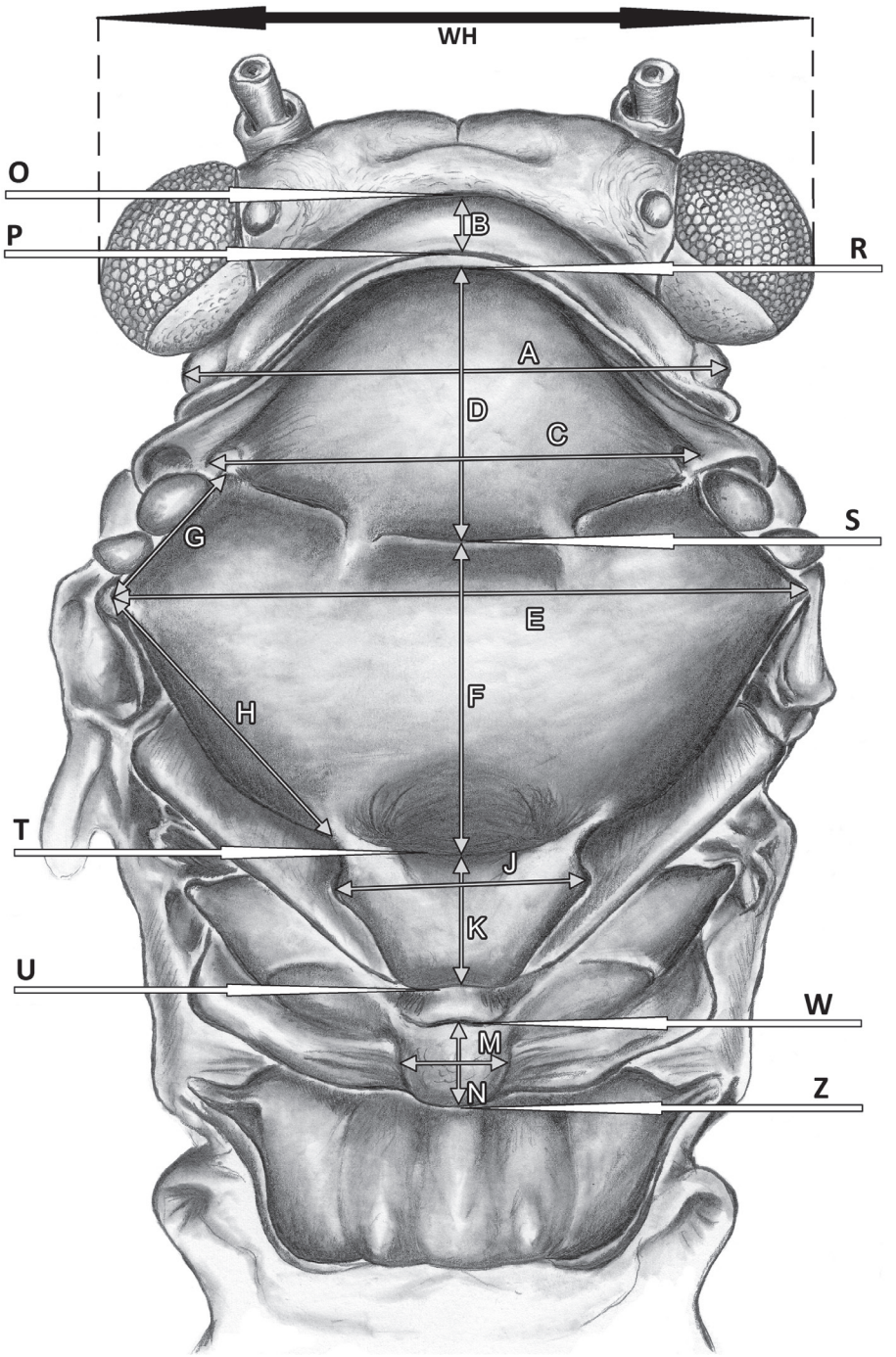


Fig. 4. Diagram of thorax dimension

Explanations: **A** – pronotum width; **B** – pronotum length; **C** – mesopraescutum width; **D** – mesopraescutum length; **E** – mesoscutum width; **F** – mesoscutum length; **G** – length of anterio-lateral margin of the mesoscutum; **H** – length of posterior-lateral margin of the mesoscutum; **J** – mesoscutellum width; **K** – mesoscutellum length; **M** – metascutellum width; **N** – metascutellum length; **O** – anterior margin of the pronotum; **P** – posterior margin of the pronotum; **R** – anterior margin of the mesopraescutum; **S** – posterior margin of the mesopraescutum, anterior margin of the mesoscutum; **T** – posterior margin of the mesoscutum, anterior margin of the mesoscutellum; **U** – posterior margin of the mesoscutellum, anterior margin of the metascutum; **W** – posterior margin of the metascutum, anterior margin of the metascutellum; **Z** – posterior margin of the metascutellum, **WH** – head width

2 The skeleton of Psylloidea

2.1. Thorax morphology of recent psyllids

Prothorax

The prothorax of psyllids is the smallest segment of the thorax and its dorsal part is constituted by a single sclerite – the pronotum (*pronotum*, nt1, Fig. 1). The tergite is collar-like and arched and its anterior and posterior margins are parallel in the majority of species (O, P, Fig. 4). The head adjoins the entire width of the pronotum. Only in case of *Paurocephala psylloptera* (Fig. 38A), a membraneous area is observed between the posterior margin of the head and the anterior margin of the pronotum, at the dorsal side. The pronotum is usually only slightly narrower than the head including the eyes (Calophyidae Figs. 19A–22A; Carsidaridae Figs. 23A–24A; Aphalarinae Figs. 5A–10A; Spondyliaspidinae Figs. 15A–17A; Togepsyllinae Fig. 18A; Dynopsyllini Fig. 25A; Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Pachypsylla venusta* Fig. 11A; *Apsylla cistellata* Fig. 13A; *Diaphorina truncata* Fig. 30A; *Euphyllura olivina* Fig. 32A; *Camaratoscena speciosa* Fig. 36A; *Paurocephala psylloptera* Fig. 38A; *Syntomoza unicolor* Fig. 39A), or distinctly narrower than the head (Phacopteronidae Fig. 40A; Psyllidae Figs. 41A–54A; Triozidae Figs. 55A–63A; Edenini Fig. 27A; and *Psyllopsis fraxinicola* Fig. 31A). *Agonoscena pistaciae* (Fig. 12A); *Rhinocola aceris* (Fig. 14A); *Phytolyma fusca* (Fig. 29A) and *Livia junci* (Fig. 37A) constitute exceptions, as the width of their pronotum and head is similar.

In the majority of psyllid species, the anterior margin of the pronotum (O, Fig. 4) assumes the form of a more or less curved strip – from nearly straight (*Livia junci* Fig. 37A) up to U-shaped (Triozidae Figs. 55A–63A). In case of a few species the central part of the anterior margin of the pronotum is bent towards the head: Phacopteronidae (Figs. 40A, 66); *Cecidopsylla schimae* (Fig. 21A), *Caillardia robusta* (Fig. 64) and *Blastopsylla occidentalis* (Figs. 15A, 65). In *Arytaina maculata* (Fig. 48A) the anterior margin of the pronotum is also bent towards the head in its central part, but in this case the bending is smoother and forms an additional curve. Only *Mesohomotoma lineaticollis* (Fig. 23A) exhibits an anterior margin of the pronotum with 4 symmetrically distributed convexities: two at the same line as lateral ocelli and two at the anterior-lateral ends of the pronotum. The remaining analyzed species do not exhibit such convexities of the pronotum.

In most of the species, the posterior margin of the pronotum (P, Fig. 4) is arched and lacks convexities. This does not, however, concern: Phacopteronidae (Fig. 40A), *Caillardia robusta* (Fig. 64), *Apsylla cistellata* (Fig. 13A) and *Blastopsylla occidentalis* (Figs. 15A, 65), where a distinct convexity towards the head is formed. As in the case of the anterior margin, the posterior margin of the pronotum is bent to a varying extent, from nearly straight in: *Glycaspis brimblecombei* (Fig. 17A); *Livia junci* (Fig. 37A); *Arytaina maculata* (Fig. 48A), up to U-shaped (Triozidae Figs. 55A–63A).

Among all the analyzed species, a nearly rectangular and at the same time the largest pronotum is exhibited by: Carsidaridae (Figs. 23A–24A); *Livia junci* (Fig. 37A); *Glycaspis brimblecombei* (Fig. 17A) and *Caillardia robusta* (Fig. 64). The tergite in the remaining species is formed into a smoothly bent strip (Togepsyllinae Fig. 18A; Calophyinae Fig. 19A; Euphyllurini Fig. 32A; Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Aphalara polygoni* Fig. 5A; *Colposcenia jakowleffi* Fig. 7A; *Craspedolepta sonchi* Fig. 8A; *Gyropsylla spegazziniana* Fig. 9A; *Xenaphalara signata* Fig. 10A; *Agonoscena pistaciae* Fig. 12A; *Rhinocola aceris* Fig. 14A; *Mastigimas reseri* Fig. 22A; *Camaratoscena speciosa* Fig. 36A) or a distinctly arched strip as in the case of all Psyllidae (Figs. 41A–54A); Pachypsyllinae (Fig. 11A); Macrohomotominae (Figs. 27A–29A); Diaphorinini (Figs. 30A–31A); *Apsylla cistellata* (Fig. 13A); *Bharatiana octospinosa* (Fig. 20A) and *Homotoma ficus* (Fig. 26A). The most bent pronotum (U-shaped) is observed in Triozidae (Figs. 55A–63A).

In most cases, the length of the pronotum is similar, although there are species in which the central part is broader (Liviinae Figs. 36A–39A; Dynopsyllini Fig. 25A; Edenini Fig. 27A; *Blastopsylla occidentalis* Fig. 15A; *Heteropsylla cubana* Fig. 45A; *Arytaina maculata* Fig. 48A), or narrower, as in Triozidae (Figs. 55A–63A). Additionally, in case of the latter, broadenings towards the head are observed at the margins of the pronotum (Figs. 55A–63A). Only in case of *Cecidopsylla schimae* (Fig. 21A) the pronotum is not an "uniform" arched collar, but exhibits a non-typical "broken" shape.

The lateral part of the pronotum is constituted by 2 pleurites, the anterior pleurite – the proepisternum (*proepisternum*, eps1, Fig. 3) and the posterior one – the proepimeron (*proepimerum,* epm1, Fig. 3). The dimensions of the prothoracic pleurites are generally similar (Phacopteronidae Fig. 40C; almost all Psyllinae Figs. 47C–52C, 54C; Macrocorsinae Fig. 46C; Edenini Fig. 27C; *Aphalara polygoni* Fig. 5C; *Caillardia robusta* Fig. 6C; *Craspedolepta sonchi* Fig. 8C; *Gyropsylla spegazziniana* Fig. 9C; *Agonoscena pistaciae* Fig. 12C). In some species, however, the proepimeron is smaller than proepisternum (Triozidae Figs. 55C–63C; Acizziinae Fig. 41C; Aphalaroidinae Fig. 42C; Dynopsyllini Fig. 25C; Homotomini Fig. 26C; *Apsylla cistellata* Fig. 13C; *Cecidopsylla schimae* Fig. 21C; *Mesohomotoma lineaticollis* Fig. 23C and *Syntomoza unicolor* Fig. 39C) or larger than proepisternum (Pachypsyllinae Fig. 11C; Phytolymini Fig. 29C; Euphyllurini Fig. 32C; *Colposcenia jakowleffi* Fig. 7C; *Xenaphalara signata* Fig. 10C; *Mastigimas reseri* Fig. 22C; *Tenaphalara acutipennis* Fig. 24C; *Psyllopsis fraxinicola* Fig. 31C; *Paurocephala psylloptera* Fig. 38C; *Auchmerina tuthilli* Fig. 43C; *Ciriacremum nigripes* Fig. 44C).

The prothoracic pleurites are always clearly separated from each other with a propleural sulcus (*sutura propleuralis*, pls1, Fig. 3), while the boundary between them and the pronotum (*pronotum*, nt1) is not always visible. The propleural sulcus separating both the pleurites runs from the condyle of the coxa (ccx1, Fig. 3) to the pronotum (nt1), which it touches in several locations. It reaches the anterior part of the pronotum (Macrohomotominae Figs. 27C–29C; Euphyllurini Fig. 32C; Strophingiini Figs. 34C–35C; *Colposcenia jakowleffi* Fig. 7C; *Apsylla cistellata* Fig. 13C; *Rhinocola aceris* Fig. 14C; *Blastopsylla occidentalis* Fig. 15C; *Livia junci* Fig. 37C), while in other species it joins the pronotum in the central part (Carsidaridae Figs. 23C–24C; Phacopteronidae Fig. 40C; Dynopsyllini Fig. 25C; Diaphorinini Figs. 30C–31C; Ciriacreminae Figs. 43C–45C; Macrocorsinae Fig. 46C; *Aphalara polygoni* Fig. 5C; *Caillardia robusta* Fig. 6C; *Craspedolepta sonchi* Fig. 8C; *Gyropsylla spegazziniana* Fig. 9C; *Xenaphalara signata* Fig. 10C; *Pachypsylla venusta* Fig. 11C; *Agonoscena pistaciae* Fig. 12C; *Glycaspis brimblecombei* Fig. 17C; *Bharatiana octospinosa* Fig. 20C; *Cecidopsylla schimae* Fig. 21C; *Syntomoza unicolor* Fig. 39C; *Anomoneura mori* Fig. 47C; *Arytaina maculata* Fig. 48C) or reaches the posterior part of the pronotum (Triozidae Figs. 55C–63C; Psyllinae Figs. 41C–42C, 49C–54C; Togepsyllinae Fig. 18C; Calophyinae Fig. 19C; Homotomini Fig. 26C; *Mastigimas reseri* Fig. 22C; *Camaratoscena speciosa* Fig. 36C; *Paurocephala psylloptera* Fig. 38C).

In psyllids, the sternal part of the pronotum (Fig. 2) is significantly reduced and invisible due to the labium which covers that part and is partially connate with it (*labium*, li, Fig 2). The prosternum (*prosternum,* st1, Fig. 18B) is comprised of two small plates situated symmetrically at both sides of the labium, while the remaining part of the ventral side of the prothorax is membranous. Among the analyzed species, *Togepsylla matsumurana* (Fig. 18B) is the only one in which the prosternum is visible. In the remaining species, these structures were covered and impossible to observe using the proposed methods.

Three small sclerites are present between the pleurites of the prothorax and mesothorax. These are: the peritreme (*mesothoracis peritrema,* ptm2, Fig. 3), which surrounds the mesothoracic spiracle, the anterior accessory sclerite (*scleritum accessorium anterior,* aas, Fig. 3), and the posterior accessory sclerite (*scleritum accessorium posterior*, pas, Fig. 3). The peritreme with the mesothoracic spiracle is a narrow sclerite, located in the dorsovental plane, behind the proepimeron (*proepimerum*, epm1, Fig. 3) and before the mesepisternum (*mesoepisternum* eps2, Fig. 3). From above, it adjoins the anterior accessory sclerite (aas, Fig. 3), which is also narrow, but placed diagonally in relation to the long axis of the body. Anteriorly, it faces the dorsal part of the proepimeron (epm1, Fig. 3) and from the dorsal side it may reach even the pronotum. In the back, on the other hand, it adjoins the posterior accessory sclerite (pas, Fig. 3). The posterior accessory sclerite is narrow, located diagonally in relation to the long axis of the body, behind the accessory sclerite. Posteriorly it adjoins the prealar bridge (*praelare*, pbr, Fig. 3). Additional sclerites are not always easily distinguished, as they are sometimes covered by the mesepisternum appendix pointed towards the head. In all the analyzed species, the sclerite with the mesothoracic spiracle is clearly visible – with the exception of *Colposcenia jakowleffi* (Fig. 7C), in which only the anterior accessory sclerite (aas) is distinguishable. Only in the case of *Livia junci* (Fig. 37C) the remaining two sclerites besides the peritreme were impossible to observe. In the remaining analyzed species, the peritreme and at least one accessory sclerite is visible – the anterior (aas) in: Pachypsyllinae (Fig. 11C); *Apsylla cistellata* (Fig. 13C); *Triozamia lambornii* (Fig. 25C) or – the posterior (pas) in: Homotomini (Fig. 26C); Macrohomotomini (Fig. 28C). All three additional sclerites are visible in Calophyidae (Figs. 19C–22C); Carsidaridae (Figs. 23C–24C); Phacopteronidae (Fig. 40C); Psyllidae (Figs. 41C–54C); Triozidae (Figs. 55C–63C); Togepsyllinae (Fig. 18C); Euphyllurinae (Figs. 30C–32C); all species of Liviinae (Figs. 36C, 38C–39C) with one exception; Pachypsylloidini (Fig. 33C); *Aphalara polygoni* (Fig. 5C); *Caillardia robusta* (Fig. 6C); *Craspedolepta sonchi* (Fig. 8C); *Gyropsylla spegazziniana* (Fig. 9C); *Agonoscena pistacie* (Fig. 12C); *Blastopsylla occidentalis* (Fig. 15C); *Glycaspis brimblecombei* (Fig. 17C).

Mesothorax

The mesothorax is the largest part of the thorax, which is related to the functional domination of forewings over hindwings and the resulting development of the muscles that move them. As in the case of most Pterygota, the dorsal part of the mesothorax is divided into the large mesonotum and the rib-shaped mesopostnotum (*mesopostnotum,* pnt2, Fig. 1). The mesonotum is comprised of 3 sclerites: mesopraescutum (*mesopraescutum*, psc2, Fig. 1), mesoscutum (*mesoscutum*, sc2, Fig. 1) and mesoscutellum (*mesoscutellum*, scl2, Fig. 1), separated from each other with clearly visible sulci.

The mesopraescutum (psc2, Fig. 1) is located right behind the tergit of the mesothorax and its posterior margin (R, Fig. 4) always closely adjoins the posterior margin of the pronotum (nt1, Fig. 1). The lateral parts of the mesopraescutum further form the so-called prealar bridge (*praealare*, pbr, Figs. 1, 3), that is a narrow bridge which descends towards the mesepisternum, while the posterior margin of the mesopraescutum (S, Fig. 4) adjoins the mesoscutum (sc2, Fig. 1).

The mesopraescutum is usually narrower than the pronotum. The ratios of the pronotum and mesopraescutum usually range from 1.2 to 1.3 (A/C ratio, Fig. 4). In several cases, the meso-

praescutum is of the same width as the pronotum (Edenini Fig. 27A; Phytolymini Fig. 29A; *Caillardia robusta* Figs. 6A, 64; *Pachypsylla venusta* Fig. 11A; *Apsylla cistellata* Fig. 13A; *Creiis tecta* Fig. 16A).

The shape of the mesopraescutum is usually fusiform, lined diagonally in relation to the long axis of the body. In most species the ratio of width and length ranges from 1.5 to 2 (C/D ratio, Fig. 4). In part of the species (Togepsyllinae Fig. 18A; Euphyllurini Fig. 32A; Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Agonoscena pistaciae* Fig. 12A and *Rhinocola aceris* Fig. 14A) the mesopraescutum is very wide – in such cases the ratios of width and length amount to 3 or more. In some exceptional cases, the width and length of the mesopraescutum is nearly similar (e.g. *Tenaphalara acutipennis* Fig. 24A). In species from the Triozidae family (Figs. 56A–63A), the mesopraescutum is narrower than its length and assumes the shape of a triangle (the anterior margin is strongly elongated towards the head).

The mesopraescutum is significantly longer than the pronotum – in the median line the ratio of the length of the mesopraescutum and the length of pronotum ranges from 1.5 to 8.0 (D/B ratio, Fig. 4). Only *Glycaspis brimblecombei* (Fig. 17A), the *Livia junci* (Fig. 37A) and *Arytaina maculata* (Fig. 48A) exhibit a mesopraescutum that is slightly longer than the pronotum.

The shape of the posterior part of the mesopraescutum (psc2, Fig. 1) is adjusted to the anterior margin of the mesoscutum (sc2, Fig. 1), which is usually distally curved. This causes a wrong impression that the mesopraescutum overlaps the mesoscutum, although the mesopraescutum and mesoscutum are joined by posterior mesopraescutum suture (*sutura mesopraescuti posterior,* pscs, Fig. 1) and do not overlap.

The posterior mesopraescutum suture (*sutura mesopraescuti posterior*, pscs, Fig. 1) is usually deep and distinct. Only in a few species, such as Togepsyllinae (Fig. 18A); Aphalaroidinae (Fig. 42A); Pachypsyllini (Fig. 11A); Dynopsyllini (Fig. 25A); Phytolymini (Fig. 29A); Pachypsylloidini (Fig. 33A); Strophingiini (Figs. 34A–35A); *Apsylla cistellata* (Fig. 13A); *Glycaspis brimblecombei* (Fig. 17A); *Paurocephala psylloptera* (Fig. 38A); *Egeirotrioza ceardi* (Fig. 58A) and *Trioza malloticola* (Fig. 63A) the suture is shallow.

The anterior margin of the mesoscutum is usually slightly arched, but may also be nearly straight, as in Pachypsylloidini (Fig. 33A); Strophingiini (Figs. 34A–35A); *Xenaphalara signata* (Fig. 10A). There are also species in which it assumes a shape of a distinct and highly bent arc (Carsidaridae Figs. 23A–24A; Triozidae Figs. 55A–63A; Dynopsyllini Fig. 25A; Homotomini Fig. 26A and *Creiis tecta*, Fig. 16A).

In psyllids, the mesoscutum (sc2, Fig. 1) is the largest and widest sclerite of the thorax. The shape it assumes is a wide collar which is bent in such a way that the lateral parts are directed towards the head creating a U-shaped form with arms more or less broad, depending on the bending level of the anterior margin of the mesoscutum. The arms of the mesoscutum always end with a wide straight margin formed between the anterior-lateral and posterior-lateral mesoscutum angle. The parapteron (*parapterum*, ppt, Figs. 1, 3) and in some cases the adjacent tegula (*tegula*, tg, Figs. 1, 3) adjoins the anterior-lateral margin of the mesoscutum. The parapteron is located between the mesoscutum and the prealar bridge (pbr, Figs. 1, 3). In its central part, the posterior margin of the mesoscutum (T, Fig. 4) adjoins the mesoscutellum, while on its sides it forms a slightly arched section between the mesoscutellum and the posterior-lateral angle of the mesoscutum. Because the mesoscutellum is a plate which is more convex than the mesoscutum, one may be under the impression that the mesoscutellum overlaps the mesoscutum. These, however, are situated at the same height and are joined by the mesoscutum suture (*sutura mesoscuti,* scs, Fig. 1).

In most species, the mesoscutum is usually 2 or 3 times wider in relation to its length (E/F ratio, Fig. 4). Sometimes the tergite is over 4 times wider in relation to the length (Pachypsylloidini Fig. 33A; *Rhinocola aceris* Fig. 14A) or narrow as in *Tenaphalara acutipennis* (Fig. 24A) and *Triozamia lambornii* (Fig. 25A), when the ratio is lower than 2.

The anterior margin of the mesoscutum (S, Fig. 4) is archedly bent in the distal direction, but when it is nearly straight, the mesoscutum assumes hexagonal shape (Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Xenaphalara signata* Fig. 10A; *Agonoscena pistacie* Fig. 12A).

When the length of the mesoscutum, measured in the central axis is equal to the length of the lateral margin (F/G ratio, Fig. 4), the tergite is in the shape of an even, arched collar (Togepsyllinae, Fig. 18A). The length of the mesonotum is usually approximately 1.5 times higher than the length of the margin of the mesoscutum. In the Dynopsyllini species (Fig 25A) and in *Tenaphalara acutipennis* (Fig. 24A), the mesoscutum measured in the mid line is two times longer than its lateral line.

The length of the mesoscutum corresponds to or slightly exceeds the length of the mesopraescutum. In some species, the mesoscutum is at least 1.5 times longer than the mesopraescutum (F/D ratio, Fig. 4) (Rhinocolinae Figs. 12A–14A; Strophingiini Figs. 34A–35A; *Gyropsylla spegazziniana* Fig. 9A; *Xenaphalara signata* Fig. 10A; *Pachypsylla venusta* Fig. 11A; *Blastopsylla occidentalis* Fig. 15A; *Glycaspis brimblecombei* Fig. 17A; *Togepsylla matsumurana* Fig. 18A; *Euphyllura olivina* Fig. 32A; *Pachypsylloides reverendus* Fig. 33A oraz *Livia junci* Fig. 37A).

The ratio of the posterior and the lateral margin of the mesoscutum (H/G ratio, Fig. 4) usually falls in the range of 1.6–2, however, species exist in which the posterior margin of the mesoscutum is relatively short or the lateral margin of mesoscutum is relatively wide – in such cases the ratio changes and amounts to 1.3 (Togepsyllinae Fig. 18A; *Apsylla cistellata* Fig. 13A; *Cecidopsylla schimae* Fig. 21A; *Mastigimas reseri* Fig. 22A).

The boundary between the mesoscutum (sc2, Fig. 1) and mesoscutellum (scl2, Fig. 1) is clearly visible in nearly all species of the Carsidaridae family (Figs. 23A–24A); Aphalarinae (Figs. 5A–8A); Pachypsyllinae (Fig. 11A); Togepsyllinae (Fig. 18A); Pachypsylloidini (Fig. 33A); Strophingiini (Figs. 34A–35A); *Apsylla cistellata* (Fig. 13A); *Rhinocola aceris* (Fig. 14A); *Cecidopsylla schimae* (Fig. 21A); *Camaratoscena speciosa* (Fig. 36A); *Livia junci* (Fig. 37A); *Ciriacremum nigripes* (Fig. 44A); *Bactericera bielawskii* (Fig. 55A); *Bactericera curvatinervis* (Fig. 56A); *Trichochermes walkeri* (Fig. 59A) and *Trioza galii* (Fig. 62A). Weakly distinguishable boundary between the mesoscutum and mesoscutellum is characteristic to: Homotomidae (Figs. 25A–29A); Phacopteronidae (Fig. 40A); Psyllidae (Figs. 41A–43A, 45A–54A); Triozidae (Figs. 57A–58A, 60A–61A, 63A); Spondyliaspidinae (Figs. 15A–17A); Calophyinae (Fig. 19A); Euphyllurini (Fig. 32A); *Gyropsylla spegazziniana* (Fig. 9A); *Xenaphalara signata* (Fig. 10A); *Agonoscena pistaciae* (Fig. 12A); *Bharatiana octospinosa* (Fig. 20A); *Mastigimas reseri* (Fig. 22A); *Psyllopsis fraxinocola* (Fig. 31A); *Paurocephala psylloptera* (Fig. 38A); *Syntomoza unicolor* (Fig. 39A).

The mesoscutellum (scl2) is a square plate, significantly smaller than the mesoscutum behind which it is located. Symmetrical and narrow strips, the so-called axillary cords (*frenulum squamulare mesothoracis*, axc2, Fig. 1) protrude out of it in distal angles and run diagonally to partially join the mesepimeral sclerites. The axillary cord on the mesothorax (axc2) is the place where the mesonotum ends, and the wing base articulation.

The mesoscutellum (scl2, Fig. 1) usually assumes the shape of a narrow or wide trapezoid, but may also occur in a rectangular form. Mesoscutellum in the shape of a narrow trapezoid is observed in Phacopteronidae (Fig. 40A); Triozidae (Figs. 55A–63A); Macrohomotomini (Fig. 28A); Euphyllurini (Fig. 32A); *Glycaspis brimblecombei* (Fig. 17A); *Tenaphalara acutipennis* (Fig. 24A) and *Livia junci* (Fig. 37A). In remaining analyzed species, the mesoscutellum is a wide trapezoid (Calophyidae Figs. 19A–22A; Psyllidae Figs. 41A–54A; Pachypsyllinae Fig. 11A; Rhinocolinae Figs. 12A–14A; Homotomini Fig. 26A; Phytolymini Fig. 29A; Diaphorinini Figs. 30A–31A; Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Aphalara polygoni* Fig. 5A; *Caillardia robusta* Fig. 6A; *Blastopsylla occidentalis* Fig. 15A; *Creiis tecta* Fig. 16A; *Togepsylla matsumurana* Fig. 18A; *Mesohomotoma lineaticollis* Fig. 23A; *Camaratoscena speciosa* Fig. 36A; *Paurocephala psylloptera* Fig. 38A; *Syntomoza*

unicolor Fig. 39A) or a wide rectangle (Edenini Fig. 27A; *Colposcenia jakowleffi* Fig. 7A; *Craspedolepta sonchi* Fig. 8A; *Gyropsylla spegazziniana* Fig. 9A; *Xenaphalara signata* Fig. 10A). *Triozamia labornii* (Fig. 25A) constitutes an exception due to its U-shaped mesoscutellum.

The posterior margin of the mesoscutellum (U, Fig. 4) is usually straight, with the exception of species with an incisure in its posterior part: Psyllinae (Figs. 47A–54A) and *Bharatiana octospinosa* (Fig. 20A).

In its central part, at the dorsal side, the mesopostnotum (*mesopostnotum,* pnt2, Fig. 1) (situated behind the mesonotum) is covered by the mesoscutellum located in the front (scl2, Fig. 1). The lateral parts of the mesopostnotum (if visible) assume a shape of irregular plates.

The lateral walls of the mesothorax comprise of two large sclerites: the anterior sclerite – mesepisternum (*mesepisternum,* eps2, Fig. 3) and the posterior sclerite – mesoepimerum (*mesoepimerum*, epm2, Fig. 3). Both the sclerites are incompletely separated by a mesopleural sulcus (*sutura mesopleuralis* pls2, Fig. 3). The mesopleural suture runs from the condyle of coxa and approaches the central point of the mesopleuron, but never reaches the base of the wing. In psyllids, the position and shape of the mesopleural suture is highly variable. In most of the species, the mesopleural suture is short, delicate and oblique (Phacopteronidae Fig. 40C; Triozidae Figs. 55C–63C; Calophyinae Fig. 19C; Rhinocolinae Fig. 12C–14C; Pachypsyllini Fig. 11C; Diaphorinini Figs. 30C–31C; Euphyllurini Fig. 32C; *Caillardia robusta* Fig. 6C; *Togepsylla matsumurana* Fig. 18C; *Cecidopsylla schimae* Fig. 21C; *Mastigimas reseri* Fig. 22C; *Paurocephala psylloptera* Fig. 38C; *Syntomoza unicolor* Fig. 39C). There are, however, species with relatively long, distinct oblique suture, such as Carsidaridae (Figs. 23C–24C); Homotomidae (Figs. 25C–29C); Macrocorsinae (Fig. 46C); Psyllinae (Figs. 47C–54C); *Colposcenia jakowleffi* (Fig. 7C); *Bharatiana octospinosa* (Fig. 20C) and *Auchmerina tuthilli* (Fig. 43C). Only in several species the mesopleural suture is nearly horizontal (Spondyliaspidinae Figs. 15C–17C, Aphalaroidinae Fig. 42C; Ciriacreminae Figs. 44C–45C; Pachypsylloidini Fig. 33C; Strophingiini Figs. 34C–35C; Acizziinae Fig. 41C; *Aphalara polygoni* Fig. 5C; *Craspedolepta sonchi* Fig. 8C; *Gyropsylla spegazziniana* Fig. 9C; *Xenaphalara signata* Fig. 10C; *Camaratoscena speciosa* Fig. 36C oraz *Livia junci* Fig. 37C).

In cases where the mesopleural suture is horizontal, it sometimes joins the anapleural cleft (*sutura anapleuralis* acl2, Fig. 3), as it is in the case of species of the Ciriacreminae subfamily (Figs. 43C–45C) or the *Glycaspis brimblecombei* (Fig. 17C).

The mesepisternum (*mesepisternum,* eps2, Fig. 3) assumes various shapes depending on the position and course of the mesopleural sulcus (pls2, Fig. 3) and the anapleural cleft (acl2, Fig. 3).

The anterior-dorsal part of the mesepisternum adjoins a long, narrow bridge running from the mesopraescutum in the ventral direction – the so-called prealar bridge (*praealare*, pbr, Figs. 1, 3) by means of a distinct suture – the prescutoepisternal sulcus (*sutura prescutoepisternalis*, pes, Fig. 3). Both the prealar bridge and the prescutoepisternal sulcus are well visible in all species. In all species, the anterodorsal part of the mesepisternum is convex and easily distinguishable. The anterior or anterior-ventral part of the mesepisternum is the so-called preepisternum (*proepisternum,* peps, Fig. 3). It is a narrow part that is rarely visible in psyllids, as it is usually set perpendicularly in relation to the long axis of the body and is bent towards the inside forming a vertical wall.

The anapleural cleft (*sutura anapleuralis*, acl2, Fig. 3) divides the mesepisternum into the dorsal and ventral parts. The dorsal part is called the anaepisternum (*anaepisternum*, aeps), while the ventral part is comprised of preepisternum (*proepisternum*, peps) and/or katepisternum (*katepisternum,* kes2, Fig. 3) and trochantin (*trochantinus mesothoracis*, trn2, Fig 3). It is not always possible to isolate the preepisternum, and when it is, it borders with the anaepisternum in the back and with the katepisternum in the ventral part. The katepisternum is always located below the anapleural cleft (acl2, Fig. 3) and in the anteriorly of trochantin (trn2, Fig. 3). Sometimes, the katepisternum and trochantin fully or

partially blend forming the so-called katepisternal complex. The katepisternum (kes2, Fig. 3) is usually rounded (oval) and striated. It is usually easily distinguishable, assumes various shapes and adjoins the basisternum at the ventral side (*basisternum,* st2, Fig. 2) in the location where the pleurosternal suture (*sutura pleurosternalis*, pss, Fig. 2) runs. In the anterior-ventral margin or in the centre of the katepisternal complex, the fossa of the trochantnal apodeme appears (*fossa apodemae trochantinalis,* ftna2, Fig. 3) in all species of psyllids and is always easily distinguishable.

The anapleural cleft of psyllids is developed to a variable extent. Usually it is very well visible, distinct, set nearly horizontally (Carsidaridae Figs. 23C–24C; Phacopteronidae Fig. 40C; Spondyliaspidinae Figs. 15C–17C; Acizziinae Fig. 41C; Aphalaroidinae Fig. 42C; Ciriacreminae Figs. 43C–46C; Dynopsyllini Fig. 25C; Homotomini Fig. 26C; Pachypsylloidini Fig. 33C; *Aphalara polygoni* Fig. 5C; *Colposcenia jakowleffi* Fig. 7C; *Craspedolepta sonchi* Fig. 8C; *Togepsylla matsumurana* Fig. 18C; *Mastigimas reseri* Fig. 22C; *Paurocephala psylloptera* Fig. 38C) or diagonally (Triozidae Figs. 55C–63C; Pachypsyllinae Fig. 11C; Psyllinae Figs. 47C–51C, 53C–54C; Edenini Fig. 27C; Macrohomotomini Fig. 28C; Diaphorinini Figs. 30C–31C; Euphyllurini Fig. 32C; *Caillardia robusta* Fig. 6C; *Gyropsylla spegazziniana* Fig. 9C; *Xenaphalara signata* Fig. 10C; *Cecidopsylla schimae* Fig. 21C; *Phytolyma fusca* Fig. 29C and *Ciriacremum nigripes* Fig. 44C). In several cases, the anapleural cleft is poorly developed, very short and faintly visible (Rhinocolinae Figs. 12C–14C; Calophyinae Fig. 19C; Liviinae Figs. 36C–37C, 39C; Pachypsylloidini Fig. 33C; Strophingiini Figs. 34C–35C and *Bharatiana octospinosa* Fig. 20C).

The mesepimeron (epm2, Fig. 3) is a structure that is more complex than the mesepisternum due to the vertical sulcus called the transepimeral sulcus (*sulcus transepimeralis*, tems, Fig. 3) that runs vertically or is slightly oblique from the dorsal coxa point to the anterior pleural angle of the anterior pleural wing process (*processus anterior alae,* apwp, Fig. 3). In most psyllids this sulcus is well developed and distinct, usually long and slightly arched. Species exist in which the transepimeral sulcus is delicate and indistinct (Carsidaridae Figs. 23C–24C; Rhinocolinae Figs. 12C–14C; Togepsyllinae Fig. 18C; Calophyinae Fig. 19C; Liviinae Figs. 37C–39C; Aphalaroidinae Fig. 42C; Ciriacreminae Figs. 43C, 45C; Macrocorsinae Fig. 46C; Psyllinae Figs. 47C–54C; Diaphorinini Figs. 30C–31C; Pachypsylloidini Fig. 33C and *Bharatiana octospinosa* Fig. 20C).

The widest part of the mesepimeron lies anteriorly of the transepimeral sulcus. The ventral part of the mesepimeron (epm2) forms the katepimeron (*katepimerum*, kem2). The dorsal, posterior margin of this sclerite (behind the transepimeral sulcus and anteriorly of the third peritreme) supports the base of the anterior pleural wing process (*processus anterior alae*, apwp, Fig. 3). The pleural wing process is thin and horizontally curved. It connects the anterior part of the wing base with the centre of the dorsal margin of the mesopleuron. The pleural process of the wing (apwp) is ended with the heel of the epimeron (*calx epimeri*, hepm, Fig. 3), a structure that is easily distinguishable, joined with the mesopostnotum (ptn2) at its posterior part. The heel of the epimeron constitutes the posterodorsal margin of the mesopleuron. In all species, there is a cavity behind the heel of epimeron (hepm, Fig. 3), which clearly separates the mesepimeron from the peritreme and touches the mesopostnotum (pnt2, Fig. 3) in the dorsal part.

Two round, protruding structures occur behind the prealar bridge: the frontal, larger structure – the so-called parapteron (*parapterum*, ppt, Fig. 3) and the posterior structure – the so-called tegula (*tegula*, tg, Fig. 3). The parapteron is located between the prealar bridge (pbr), the mesopraescutum (psc2), the mesoscutum (sc2) and the tegula (tg). The tegula, on the other hand, lies at the dorsal margin of the mesepisternum, the so-called basalare (*basalare*, bas, Fig. 3), directly before the remaining elements comprising the wing base articulation.

Usually the parapteron is a convex and oval structure, with the exception of Dynopsyllini (Fig. 25C), which it assumes the shape of a heart due to the convexity in the lateral part, as well

as Strophingiini (Figs. 34C–35C); *Rhinocola aceris* (Fig. 14C); *Euphyllura olivina* (Fig. 32C) and *Livia junci* (Fig. 37C), where it assumes a form of a flattened, irregular plate.

In most species, the parapteron is larger than the tegula (sometimes twice as large), but species exist in which the sizes of these structures are comparable: Calophyinae (Fig. 19C); *Craspedolepta sonchi* (Fig. 8C); *Paurocephala psylloptera* (Fig. 38C); *Syntomoza unicolor* (Fig. 39C).

As in the case of the parapteron, the tegula is usually oval in shape and may also assume the shape of a flat plate, thus adjusting to the parapteron, e.g.: Strophingiini (Figs. 34C–35C); *Rhinocola aceris* (Fig. 14C); *Euphyllura olivina* (Fig. 32C) oraz *Livia junci* (Fig. 37C).

Contrary to the prothorax, the sternal part of the mesothorax in psyllids is well distinguishable. It is relatively highly scleritized, yet the boundaries between individual elements are not always evident.

In the centre of the ventral part of the mesothorax, a convex basisternum (*basisternum*, st2, Fig. 2) is usually located, a plate characterized by high variability of dimensions and shapes in case of psyllids. The middle part of the anterior margin of basisternum touches the rostrum (*labium*, li, Fig. 2), the end of which is located between the procoxa. The anterior-lateral parts of the basisternum adjoin the katepisternum (*katepisternum*, kes2, Figs. 2–3) and are separated from them by the pleurosternal suture (*sutura pleurosternalis*, pss, Fig. 2). The suture is visible to a higher or lower extent in individual species. It runs diagonally or arcwise causing the basisternum to assume a more or less oval shape.

The posterior part of the basisternum touches the short, arched arms of a V-shaped suture, namely the sternocostal suture (*sutura sternocostalis*, stcx, Fig. 2), the narrow end of which constitutes the base for furcae. The furcal pit on mesothorax is not visible at the surface of the furcasternum. That part of the sternite is very narrow and reduced. In some species, a distinct convexity is formed anteriorly of the mesocoxa (*mesocoxa*, cx2, Fig. 2), seemingly located at the extension of the strernocostal suture. It is located behind the katepisternum (kes2, Fig. 2) and it seems to be the convexity of the trochantin, the main part of which, including the suture, is located above, on the lateral wall of the body (*trochantinus mesothoracis*, trn2, Fig. 3). Such a convexity occurs in: Psyllidae (Figs. 41B–54B); Triozidae (Figs. 55B–63B); Euphyllurini (Fig. 32B); *Psyllopsis fraxinicola* (Fig. 31B); *Paurocephala psylloptera* (Fig. 38B) and *Syntomoza unicolor* (Fig. 39B).

The anterior margin of the mesosternum formed by the anterior margin of the basisternum and the anteroventral parts of the katepisternum is usually a gentle, depressed arc, but may also be straight and devoid of any convexities (Spondyliaspidinae Figs. 15B–17B; *Apsylla cistellata* Fig. 13B). In some species, the anteroventral parts of katepisternum are directed towards the head to such an extent that the anterior margin of the mesosternum is strongly incised in the middle (Carsidaridae Figs. 23B–24B; Phacopteronidae Fig. 40B; Calophyinae Fig. 19B; Phytolymini Fig. 29B; *Aphalara polygoni* Fig. 5B; *Gyropsylla spegazziniana* Fig. 9B; *Mastigimas reseri* Fig. 22B and *Livia junci* Fig. 37B).

The basisternum (st2, Fig. 2) is usually a plate with marked boundaries between the former and the katepisternum (kes2, Fig. 2), where the pleurosternal suture (pss, Fig. 2) is clearly visible. In some species, the suture may be barely visible as a slight recess (Calophyidae Figs. 19B–22B; Pachypsyllinae Fig. 11B; Macrohomotomini Fig. 28B; Pachypsylloidini Fig. 33B; Strophingiini Figs. 34B–35B; *Aphalara polygoni* Fig. 5B; *Colposcenia jakowleffi* Fig. 7B, *Gyropsylla spegazziniana* Fig. 9B; *Xenaphalara signata* Fig. 10B; *Rhinocola aceris* Fig. 14B; *Blastopsylla occidentalis* Fig. 15B; *Glycaspis brimblecombei* Fig. 17B; *Euphalerus vittatus* Fig. 46B; *Anomoneura koreana* Fig. 47B; *Arytaina maculata* Fig. 48B) or invisible (Rhinocolinae Figs. 12B–13B; Togepsyllinae Fig. 18B; Pachypsylloidini Fig. 33B; *Caillardia robusta* Fig. 6B and *Creiis tecta* Fig. 16B).

The basisternum is usually triangular (Phacopteronidae Fig. 40B; Triozidae Figs. 55B–63B; Acizziinae Fig. 41B; Aphalaroidinae Fig. 42B; Homotomini Fig. 26B; Strophingiini Figs. 34B–35B; *Gyropsylla spegazziniana* Fig. 9B; *Xenaphalara signata* Fig. 10B; *Blastopsylla occidentalis* Fig. 15B; *Glycaspis brimblecombei* Fig. 17B; *Diapho-*

rina truncata Fig. 30B; *Camaratoscena speciosa* Fig. 36B; *Syntomoza unicolor* Fig. 39B; *Arytaina maculata* Fig. 48B; *Ciriacremum nigripes* Fig. 44B; *Cyamophila bajevae* Fig. 52B; *Psylla foersteri* Fig. 53B), but it may also assume the rhomboid shape (Carsidaridae Figs. 23B–24B; *Aphalara polygoni* Fig. 5B; *Colposcenia jakowleffi* Fig. 7B). The basisternum may sometimes assume an oval shape, as in: Calophyinae (Fig. 19B); Mastigimatinae (Figs. 21B–22B); Macrocorsinae (Fig. 46B); Psyllinae (Figs. 47B, 49B–51B, 54B); Macrohomotomini (Fig. 28B); Phytolymini (Fig. 29B); *Craspedolepta sonchi* (Fig. 8B); *Psyllopsis fraxinicola* (Fig. 31B); *Paurocephala psylloptera* (Fig. 38B); *Auchmerina tuthilli* (Fig. 43B); *Heteropsylla cubana* (Fig. 45B); or be mushroom-shaped as in *Bharatiana octospinosa* (Fig. 20B) and *Livia junci* (Fig. 37B). In case of the barely visible pleurosternal suture, the shape of the basisternum is impossible to identify (Rhinocolinae Figs. 12B–14B; Togepsyllinae Fig. 18B; Pachypsyllini Fig. 11B; Pachypsylloidini Fig. 33B; *Caillardia robusta* Fig. 7B; *Creiis tecta* Fig. 16B).

In its anterior part, the mesosternum is broadened. This is caused by the specific setting and shape of the katepisternum (kes2, Fig. 2). The lateral parts of the katepisternum are usually set in such a way that they do not exceed the width of the head (Phacopteronidae Fig. 40B; Psyllidae Figs. 41B–54B; Triozidae Figs. 55B–63B; Calophyinae Fig. 19B; Liviinae Figs. 36B–37B, 39B; Euphyllurini Fig. 32B; Strophingiini Figs. 34B–35B; *Aphalara polygoni* Fig. 5B; *Colposcenia jakowleffi* Fig. 7B; *Craspedolepta sonchi* Fig. 8B; *Rhinocola aceris* Fig. 14B; *Mastigimas reseri* Fig. 22B; *Psyllopsis fraxinicola* Fig. 31B), but in some species they exhibit similar width as the head including the eyes: Togepsyllinae (Fig. 18B); Pachypsylloidini (Fig. 33B); *Caillardia robusta* (Fig. 6B); *Gyropsylla spegazziniana* (Fig. 9B); *Agonoscena pistacie* (Fig. 12B) and *Diaphorina truncata* (Fig. 30B). In a group of species the katepisternum exceeds the width of the head: Carsidaridae (Figs. 23B–24B); Pachypsyllinae (Fig. 11B); Spondyliaspidinae (Figs. 15B–17B); Mastigimatinae (Figs. 20B–21B); Edenini (Fig. 27B); Phytolymini (Fig. 29B); *Xenaphalara signata* (Fig. 10B) and *Apsylla cistellata* (Fig. 13B).

In its anteroventral part, the katepisternum may be more or less elongated. In such cases it assumes the shape of plates propagating from the basisternum at its ventral side. These may shape variously. Small oval plates occur in species such as: Triozidae (Figs. 55B–63B); Rhinocolinae (Figs. 12B–14B); Spondyliaspidinae (Figs. 15B–17B); Togepsyllinae (Fig. 18B); Edenini (Fig. 27B); Macrohomotomini (Fig. 28B); Strophingiini (Figs. 34B–35B); *Xenaphalara signata* (Fig. 10B); *Ciriacremum nigripes* (Fig. 44B) and *Arytaina maculata* (Fig. 48B). The plates may be larger, with oval ends (Phacopteronidae Fig. 40B; Calophyinae Fig. 19B; Psyllinae Figs. 47B and 49B–50B; Homotomini Fig. 26B; Phytolymini Fig. 29B; Diaphorinini Figs. 30B–31B; *Gyropsylla spegazziniana* Fig. 9B; *Bharatiana octospinosa* Fig. 20B; *Tenaphalara acutipennis* Fig. 24B; *Paurocephala psylloptera* Fig. 38B; *Syntomoza unicolor* Fig. 39B; *Auchmerina tuthilli* Fig. 43B) or ending with a sharp edge – as in the case of: Pachypsyllinae (Fig. 11B); Mastigimatinae (Figs. 21B–22B); Acizziinae (Fig. 41B); Aphalaroidinae (Fig. 42B); Macrocorsinae (Fig. 46B); Psyllinae (Figs. 51B–54B); Euphyllurini (Fig. 32B); Pachypsylloidini (Fig. 33B); *Aphalara polygoni* (Fig. 5B); *Caillardia robusta* (Fig. 6B); *Colposcenia jakowleffi* (Fig. 7B); *Mesohomotoma lineaticollis* (Fig. 23B); *Camaratoscena speciosa* (Fig. 36B); *Livia junci* (Fig. 37B) and *Heteropsylla cubana* (Fig. 45B).

Metathorax

In the dorsal and ventral part, the metathorax of psyllids is unevenly developed. As the muscles moving the hindwings are significantly less developed than the muscles of the forewings, the dorsal part that contains them is relatively small. On the other hand, the ventral part of the mesothorax containing powerful muscles of the jumping legs of the third pair (characteristic to psyllids) is well developed. The dorsal side of the metathorax is comprised of the metanotum and the metapostnotum (*metapostnotum*, pnt3, Fig. 1) Within the metanotum, two tergites may be distinguished – the metascutum (*metascutum*,

sc3, Fig. 1) and the metascutellum (*metascutellum*, scl3, Fig. 1).

The metascutum (sc3, Fig. 1) is a small and narrow plate located slightly lower than the mesoscutellum (scl2) located before it and the metascutellum (scl3) located behind it. In some species, the metascutum may be covered by the adjacent sclerites and invisible from the dorsal side (Carsidaridae Figs. 23A–24A; Macrocorsinae Fig. 46A; Dynopsyllini Fig. 25A; Edenini Fig. 27A; Macrohomotomini Fig. 28A; *Ciriacremum nigripes* Fig. 44A). The metascutellum (scl3) is usually rectangular (Phacopteronidae Fig. 40A; Pachypsyllinae Fig. 11A; Rhinocolinae Figs. 12A–14A; Togepsyllinae Fig. 18A; Calophyinae Fig. 19A; Acizziinae Fig. 41A; Aphalaroidinae Fig. 42A; Ciriacreminae Figs. 43A–45A; Psyllinae Figs. 47A–54A; Edenini Fig. 27A; Phytolymini Fig. 29A; *Aphalara polygoni* Fig. 5A; *Caillardia robusta* Fig. 6A; *Cecidopsylla schimae* Fig. 21A; *Psyllopsis fraxinicola* Fig. 31A; *Camaratoscena speciosa* Fig. 36A; *Paurocephala psylloptera* Fig. 38A; *Syntomoza unicolor* Fig. 39A) or may assume the shape of a trapezoid (Carsidaridae Figs. 23A–24A; Triozidae 55A–63A; Spondyliaspidinae Figs. 15A–17A; Macrocorsinae Fig. 46A; Dynopsyllini Fig. 25A; Homotomini Fig. 26A; Euphyllurini Fig. 32A; Pachypsylloidini Fig. 33A; Strophingiini Figs. 34A–35A; *Colposcenia jakowleffi* Fig. 7A; *Craspedolepta sonchi* Fig. 8A; *Gyropsylla spegazziniana* Fig. 9A; *Xenaphalara signata* Fig. 10A; *Bharatiana octospinosa* Fig. 20A; *Mastigimas reseri* Fig. 22A and *Livia junci* Fig. 37A).

The metascutellum is larger than the metascutum in front of it and is always easily distinguishable due to symmetrical and narrow strips stemming out in distal angles – the so-called axillary cords (*frenulum squamulare mesothoracis*, axc3, Fig. 1), running diagonally towards the metepimeral sclerites and joining them partially (similarly as in the case of axc2 in the mesothorax). The metascutellum is usually half the width of the mesoscutellum (M/J ratio, Fig. 4) and the ratio amounts to 0.5–0.7. However, in the Triozidae (Figs. 55A–63A) and *Mycopsylla fici* (Fig. 27A), as well as in *Paurocephala psylloptera* (Fig. 38A), the metascutellum is nearly of the same width as the mesoscutellum.

With the exception of: Togepsyllinae (Fig. 18A); Calophyinae (Fig. 19A) and *Aphalara polygoni* (Fig. 5A), in which both the lengths are the same, the metascutellum, however, is always shorter than the mesoscutellum (N/K ratio, Fig. 4).

The metapostnotum (*metapostnotum*, pnt3, Fig. 1) is usually in a shape close to trapezoidal. Besides the proper metapostnotum, it often partially joins the tergite of the first segment of the abdomen.

In comparison to the mesothorax pleurites, the lateral side of the metathorax in psyllids is highly transformed. This is caused by the weak development of the hindwings and their muscles, as well as the development of muscles necessary for jumping and thus the developed apodeme of these muscles (especially the internal furcae). Moreover, in the metathorax, the coxal meron is vertically elongated causing both the anterior pleurite of the metepisternum (*metaepisternum*, eps3, Fig. 3) and the metepimeron (*metaepimerum*, epm3, Fig. 3) to dislocate and to assume the shape of a long, broadened strip that stretches over the metacoxa (*metacoxa*, cx3, Fig. 3) and runs in arcuate manner.

The metepisternum touches the metathoracic spiracle located in the front of the metathorax (stg3, Fig. 3). The spiracle is surrounded by a well visible peritreme (*metathoracis peritrema*, ptm3, Fig. 3). The area over the peritreme is recognized as the antetrior-dorsal angle of the metepisternum. Directly above that area, a thin, vertical, posterior wing process is located (*processus posterior alae*, pwp, Fig. 3), reaching the coxa of the hindwings.

In the posterior part and below the peritreme, a highly developed trochantin is located (*trochantinus metathoracis*, trn3, Fig. 3). It is vertically elongated and – in certain species – tuberculated, exhibiting distinct convexities (Psyllidae Figs. 41C–54C; Triozidae Figs. 55C–63C; Liviinae Figs. 36C–37C, 39C; Pachypsyllini Fig. 11C; Homotomini Fig. 26C; Phytolymini Fig. 29C; *Aphalara polygoni* Fig. 5C; *Gyropsylla spegazziniana* Fig. 9C and *Psyllopsis fraxinicola* Fig. 31C). The trochantin stretches along the posterior margin of the metapleuron, in the front of the coxa. The

fossa of the metathoracic trochantinal apodeme (ftna3, Fig. 3) is large and clearly visible in all species of the Psyllidae (Figs. 41C–54C) and Triozidae (Figs. 55C–63C) families.

In the posterior part of the dorsal portion of the trochantin and in the anterior part of the condyle of the metacoxa, there is a small triangular area with a foramen – the pleural apophysis (*apophysis pleuralis*, pa3, Fig. 3). This is where the metapleural sulcus (*sutura metapleuralis*, pls3, Fig. 3) begins. It is, however, mostly invisible in psyllids (with a few exceptions in which it is barely noticeable (Pachypsyllinae Fig. 11C; Rhinocolinae Figs. 12C–14C; Liviinae Figs. 37C–39C; Strophingiini Figs. 34C–35C; *Caillardia robusta* Fig. 6C; *Colposcenia jakowleffi* Fig. 7C; *Gyropsylla spegazziniana* Fig. 9C; *Xenaphalara signata* Fig. 10C). Behind the pleural sulcus, the posterior metapleurite – the metepimeron (*metaepimerum*, epm3, Fig. 3) is located, which is strongly pushed away by the enlarged coxa and the trochantin in its posterior part. Such dorsal setting and high growth of the coxa and the trochantin in psyllids requires the displacement of the pleurites. The metepimeron is displaced towards the dorsal side, in a counter-clockwise manner and overlaps the metepisternum from the top.

The metasternite is T-shaped. Narrow and highly sclerirized diagonal strips form arms and in the location of their crossing with a long strip running to the posterior part of the body, the furcal pit on metathorax is distinguishable (fp, Fig. 2). The coxa are highly developed and are equipped with the meracanthi (*meracanthus,* mcs, Figs. 2, 3). These processes are usually large, pointed and horn-shaped, with the exception of the Rhinocolinae (Figs. 12B–14B, 12C–14C); Spondyliaspidinae (Figs. 15B–17B, 15C–17C) and Togepsyllinae species (Figs. 18B, 18C).

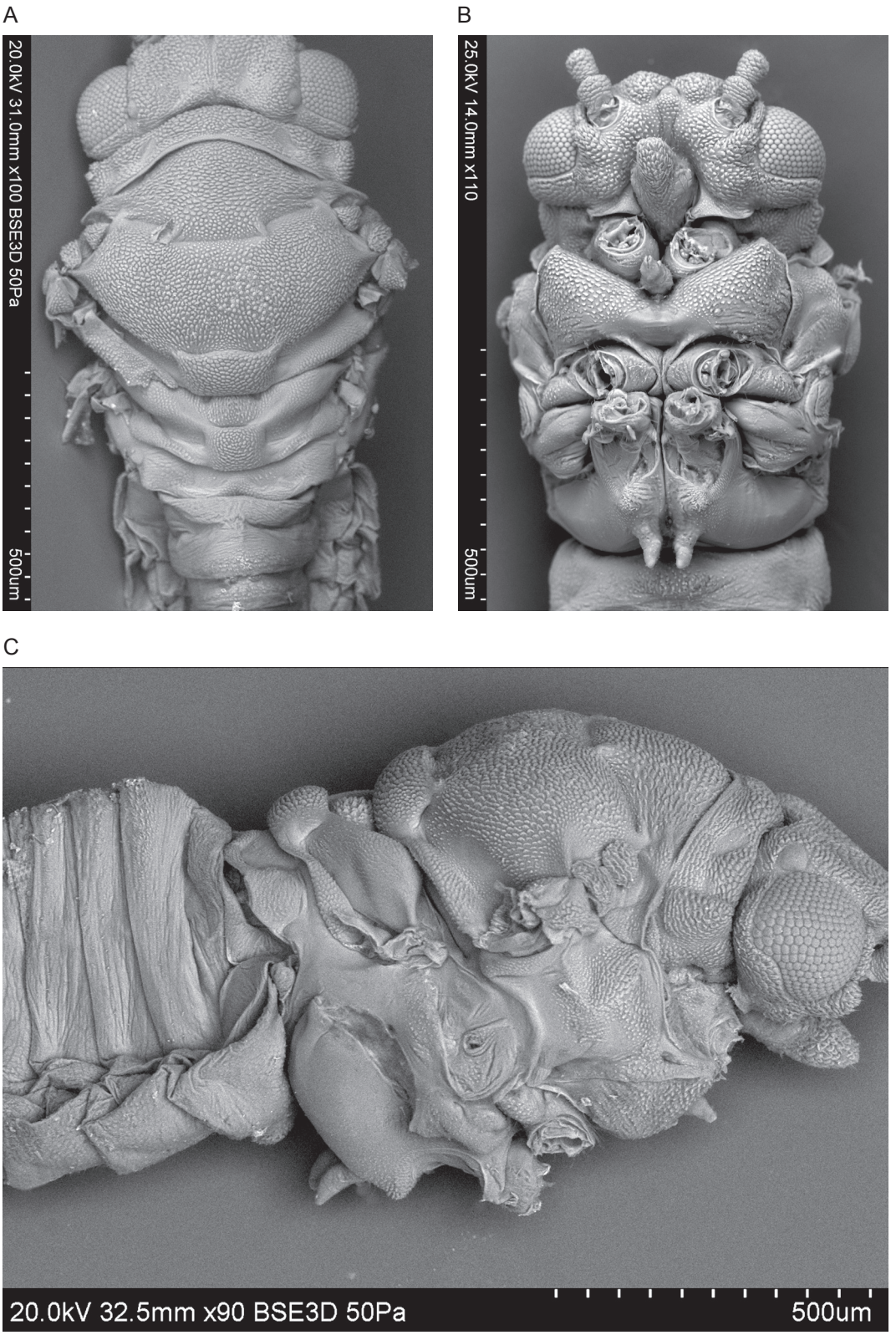


Fig. 5. *Aphalara polygoni* Foerster, 1848; **A** – dorsal side, **B** – ventral side, **C** – lateral side

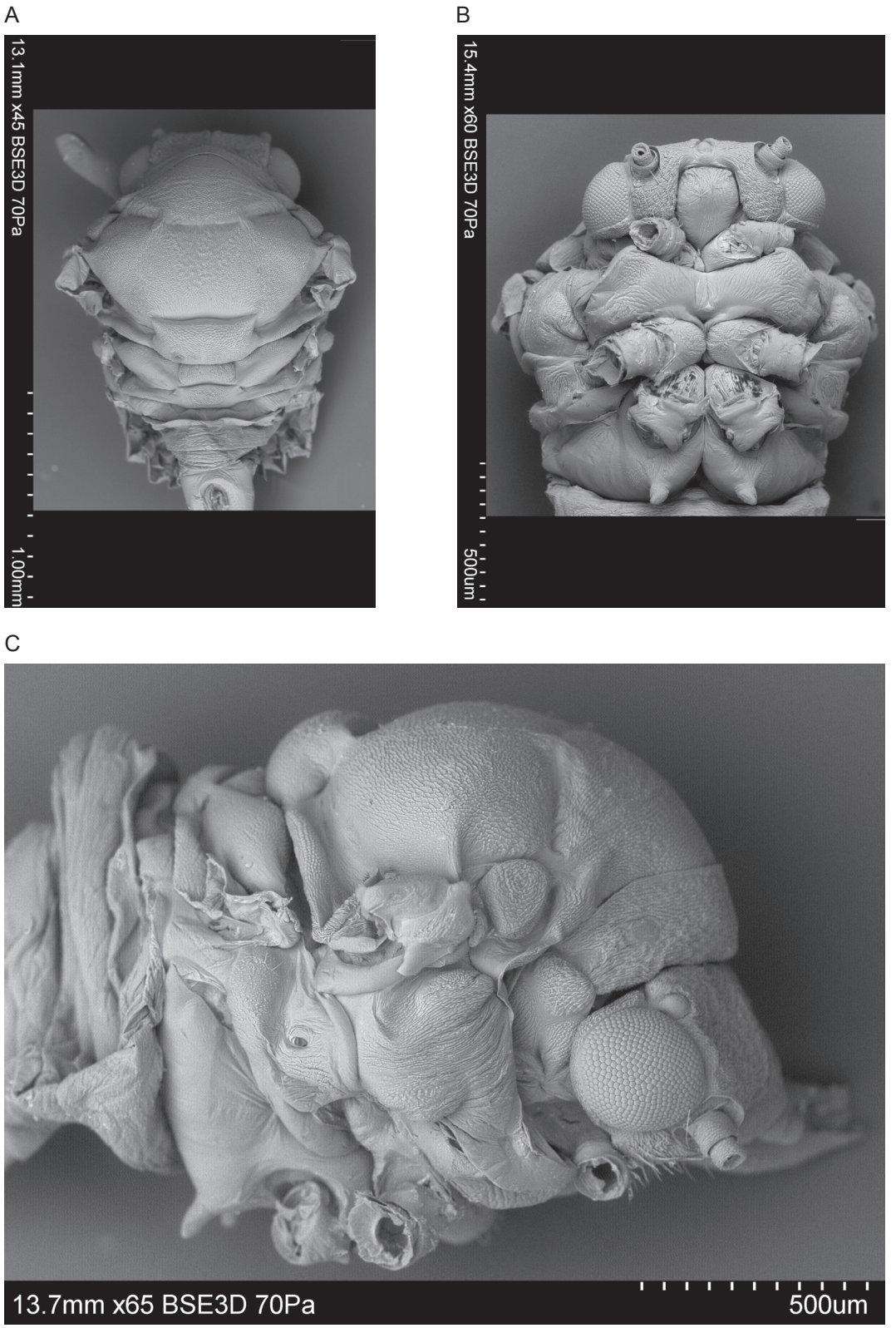


Fig. 6. *Caillardia robusta* Loginova, 1956; **A** – dorsal side, **B** – ventral side, **C** – lateral side

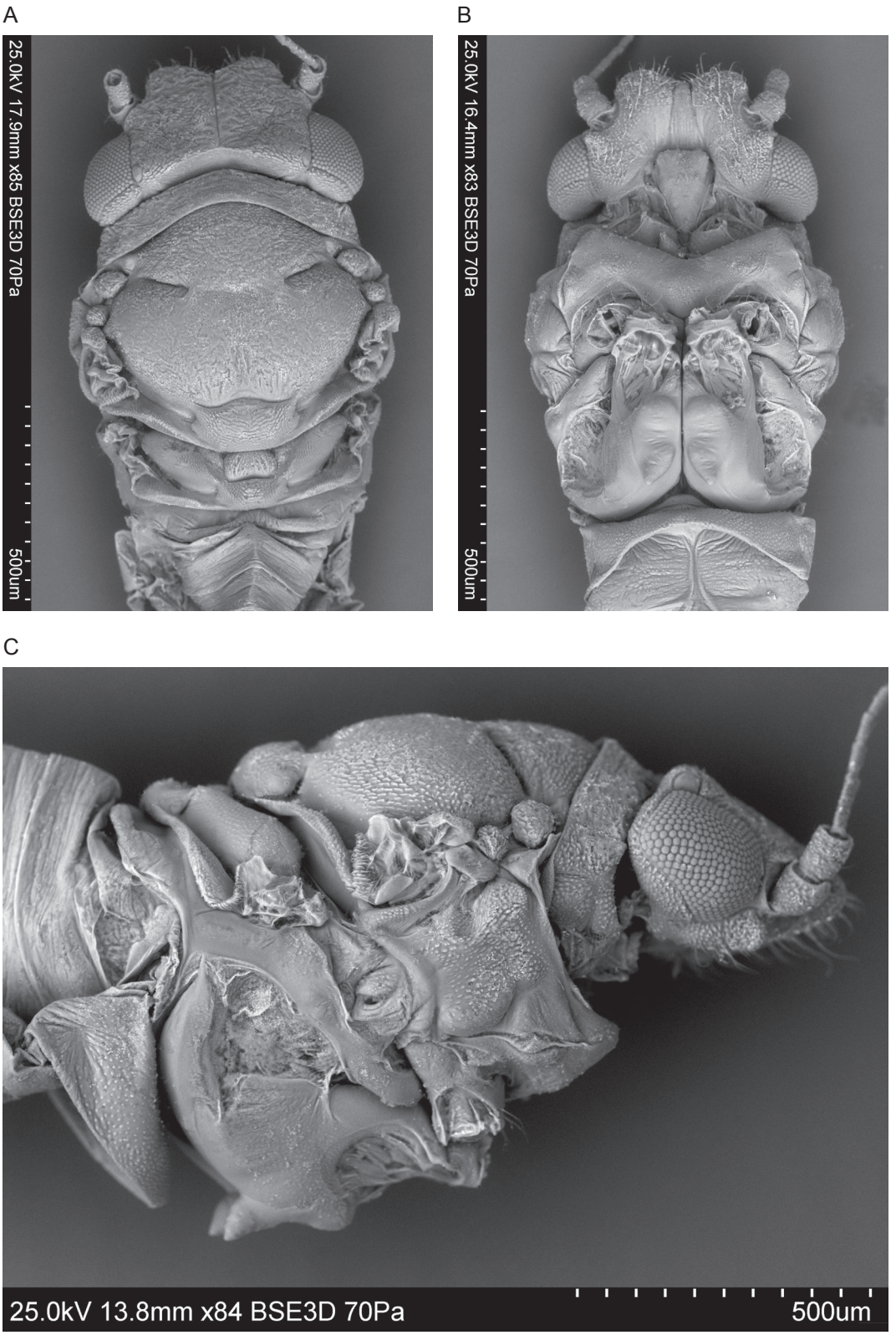


Fig. 7. *Colposcenia jakowleffi* (Scott, 1879); **A** – dorsal side, **B** – ventral side, **C** – lateral side

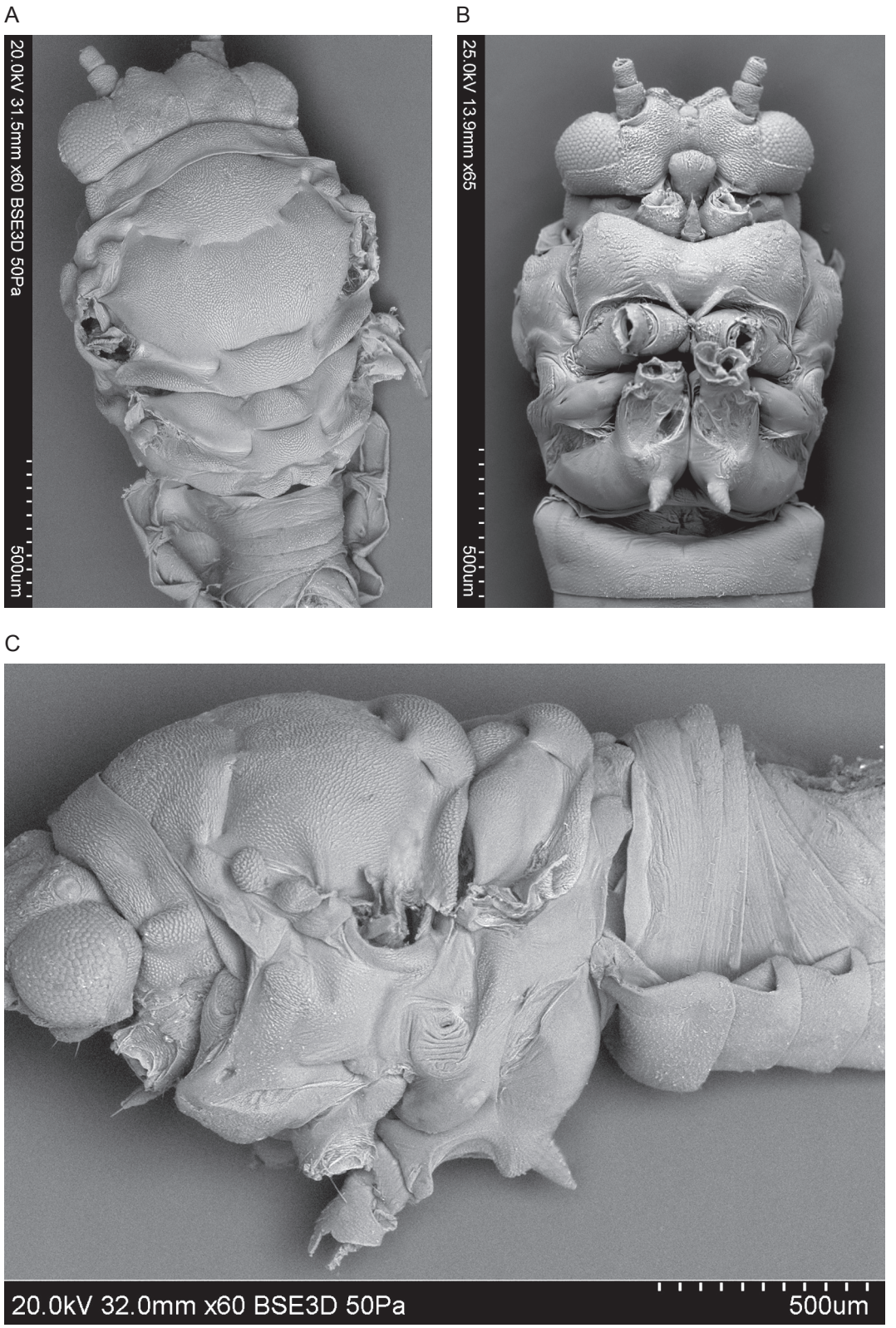


Fig. 8. *Craspedolepta sonchi* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side

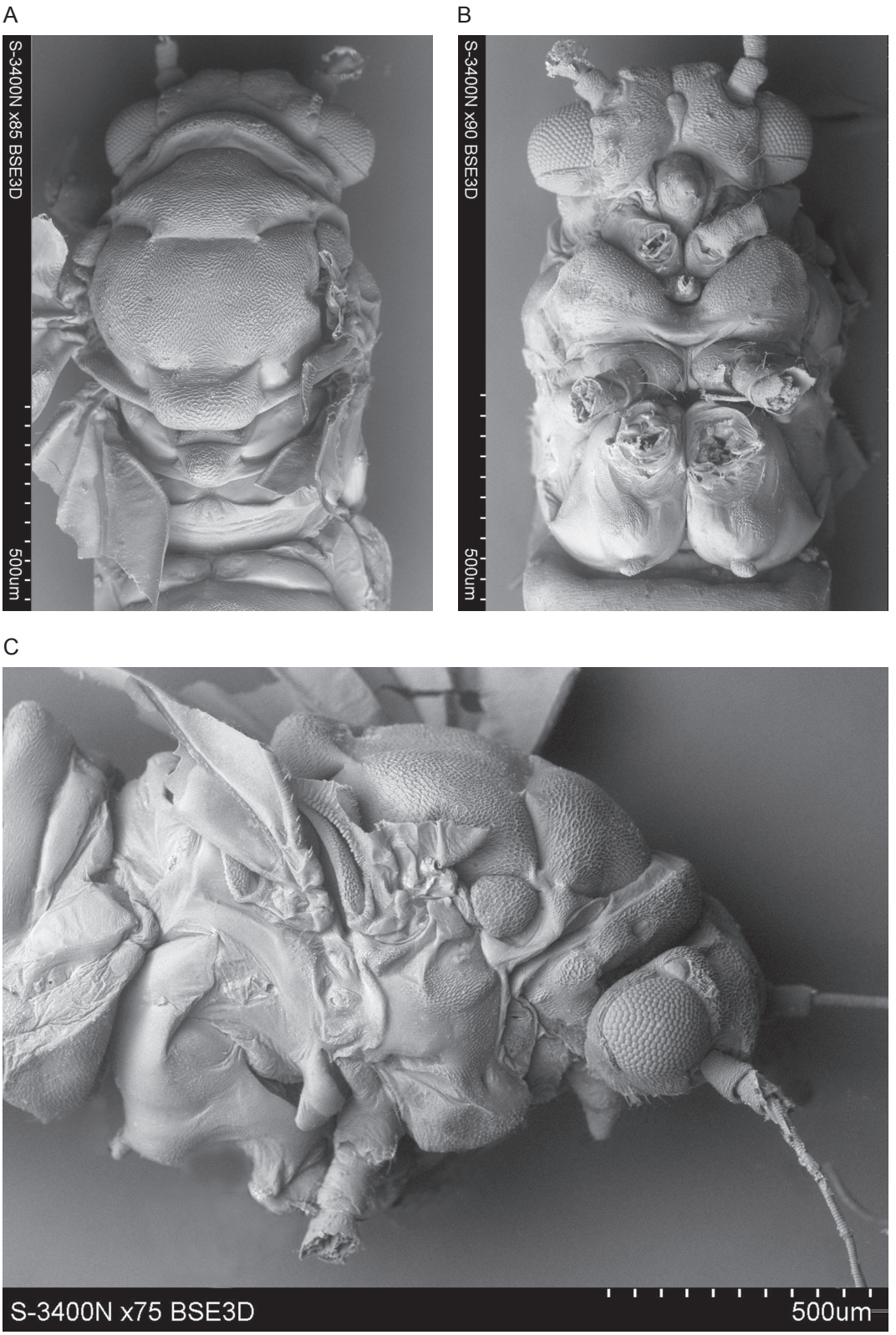


Fig. 9. *Gyropsylla spegazziniana* (Lizer, 1919); **A** – dorsal side, **B** – ventral side, **C** – lateral side

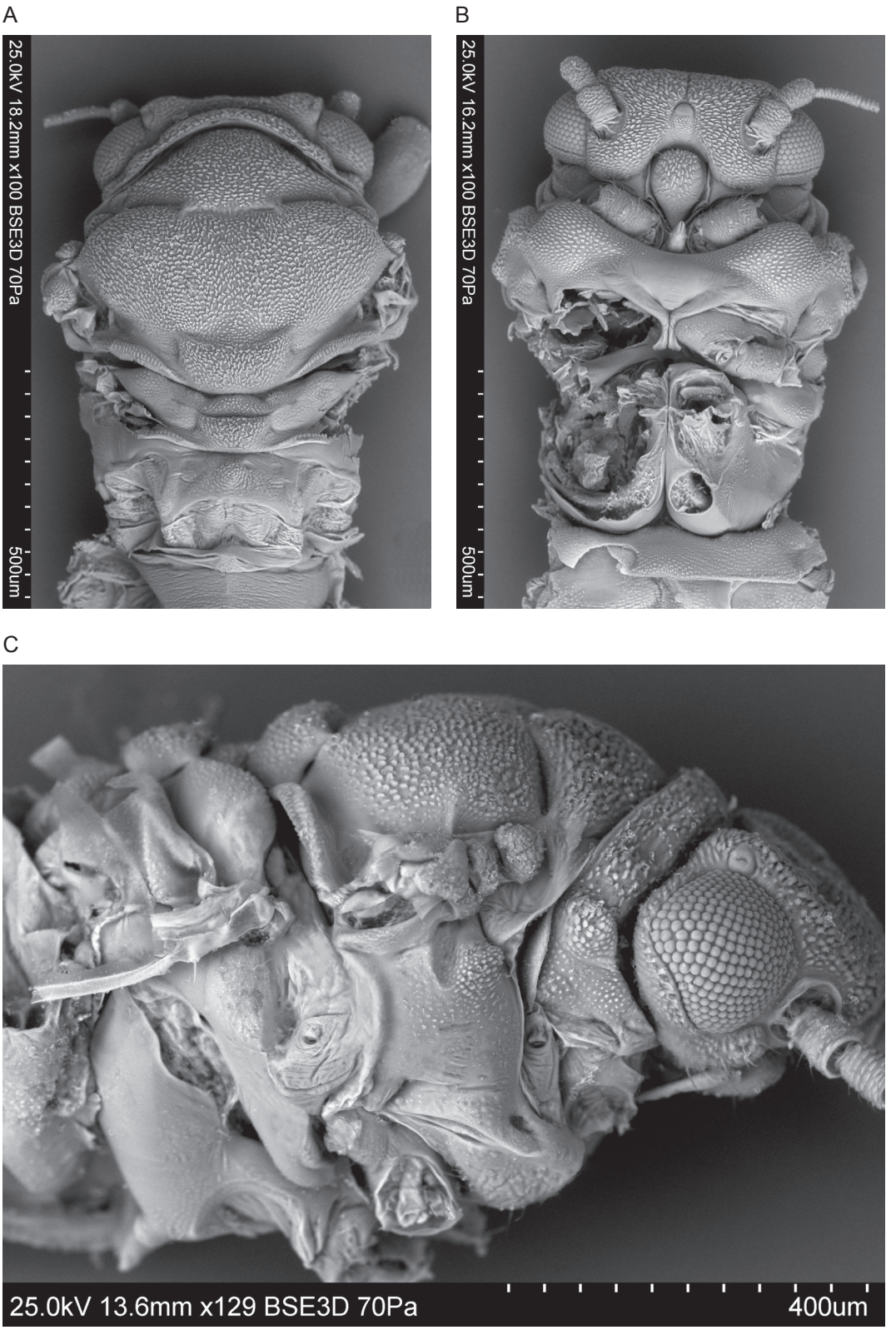


Fig. 10. *Xenaphalara signata* (Löw, 1881); **A** – dorsal side, **B** – ventral side, **C** – lateral side

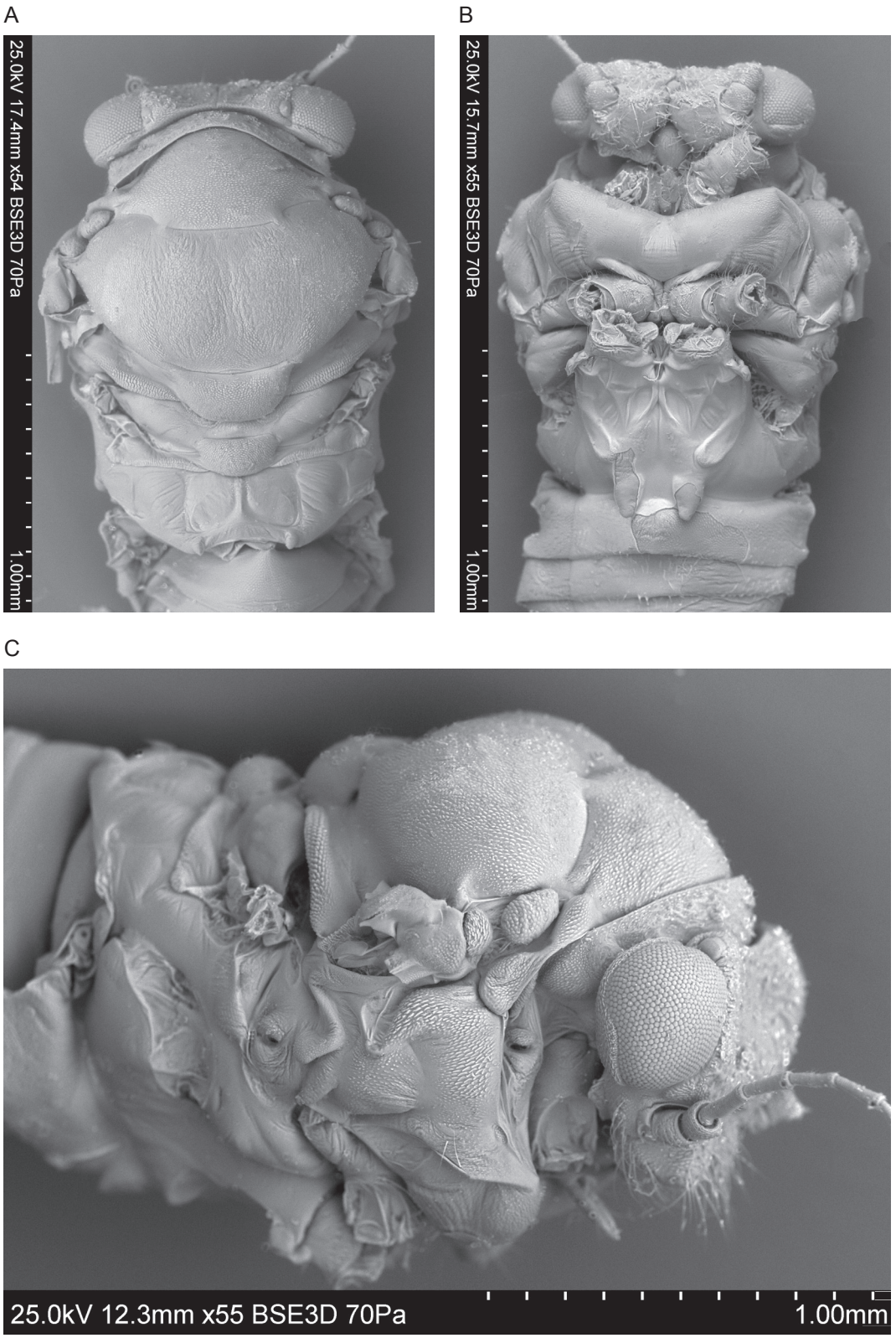


Fig. 11. *Pachypsylla venusta* (Osten-Sacken, 1861); **A** – dorsal side, **B** – ventral side, **C** – lateral side

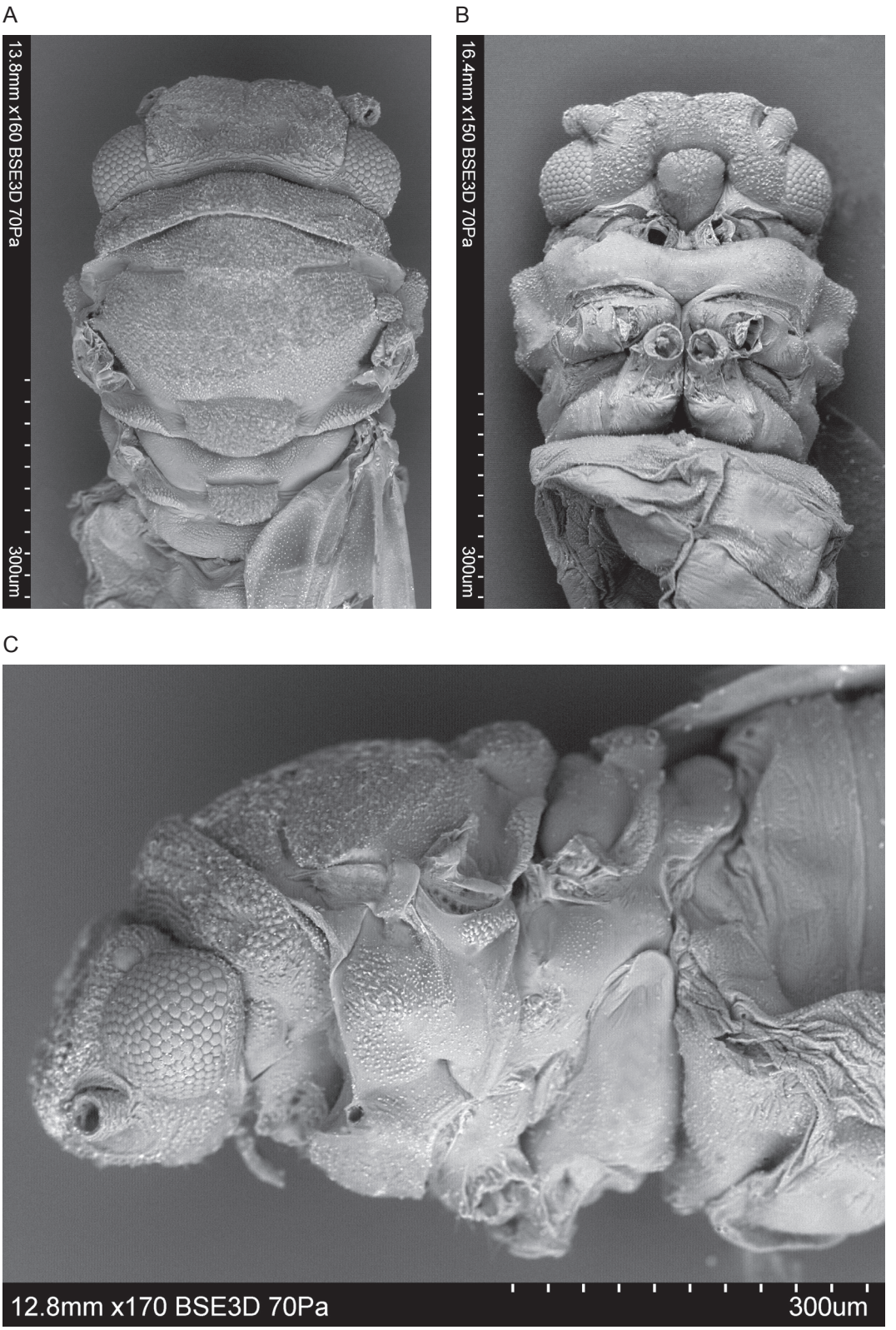


Fig. 12. *Agonoscena pistaciae* Burckhardt, Lauterer, 1989; **A** – dorsal side, **B** – ventral side, **C** – lateral side

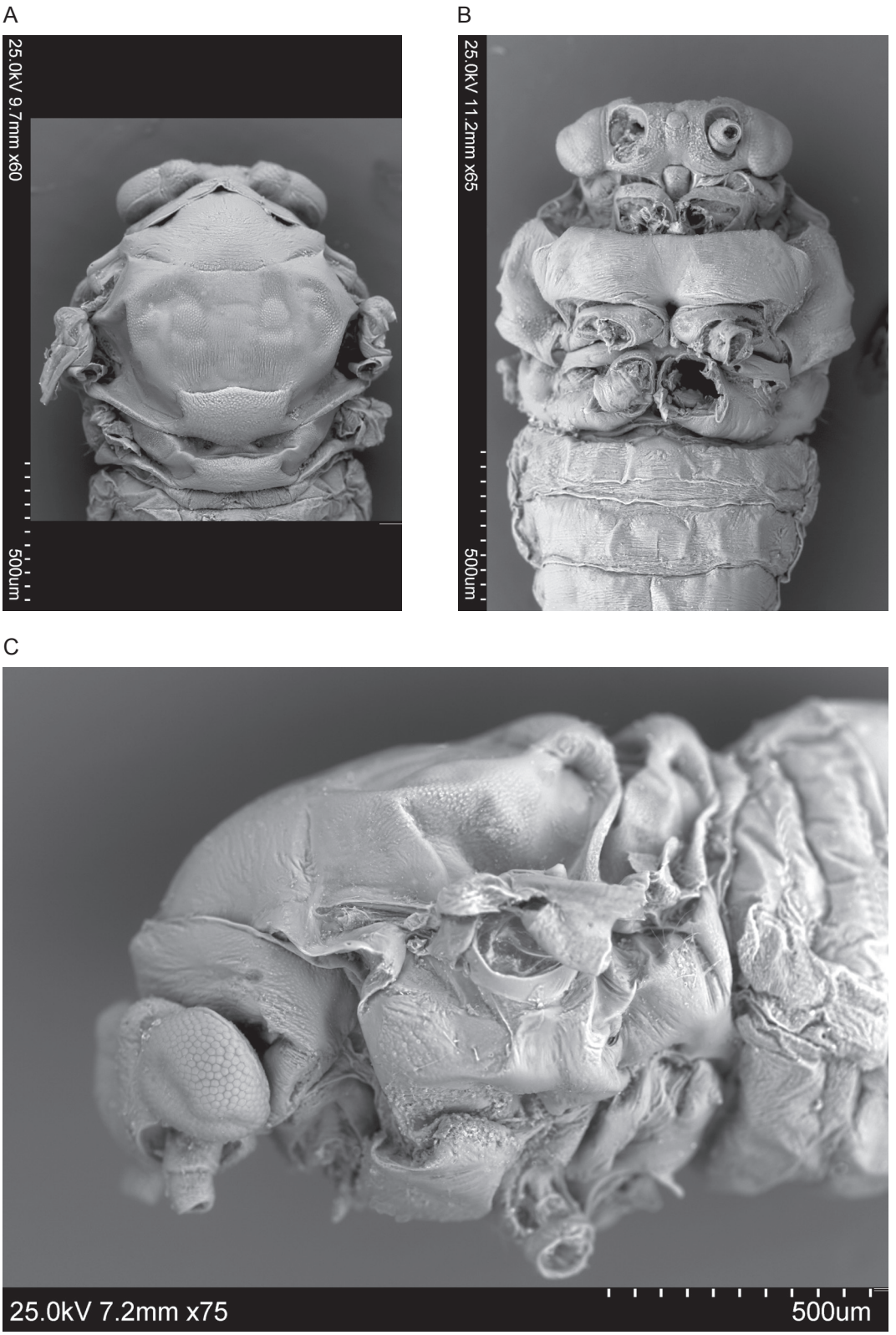


Fig. 13. *Apsylla cistellata* (Buckton, 1896); **A** – dorsal side, **B** – ventral side, **C** – lateral side

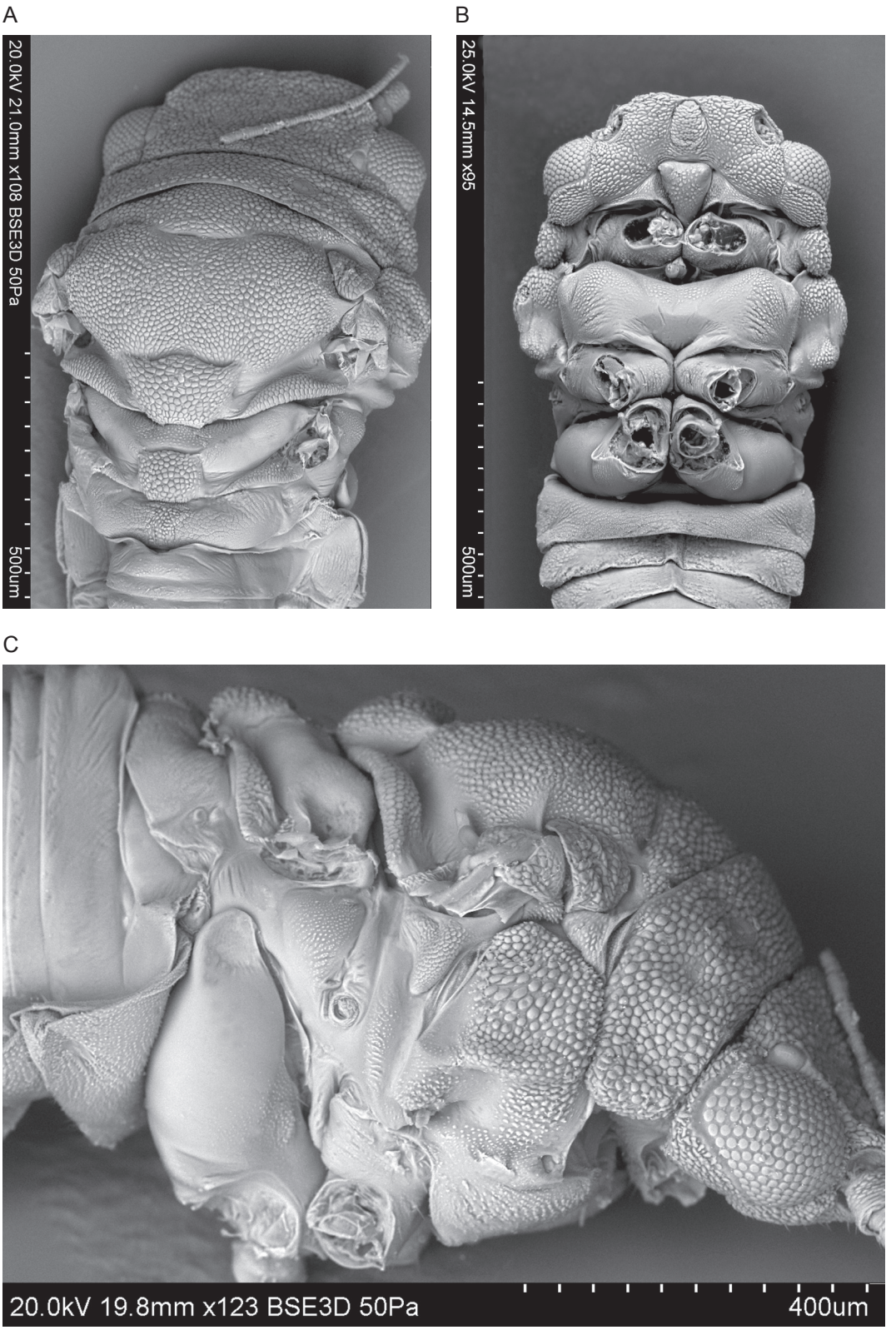


Fig. 14. *Rhinocola aceris* (Linnaeus, 1758); **A** – dorsal side, **B** – ventral side, **C** – lateral side

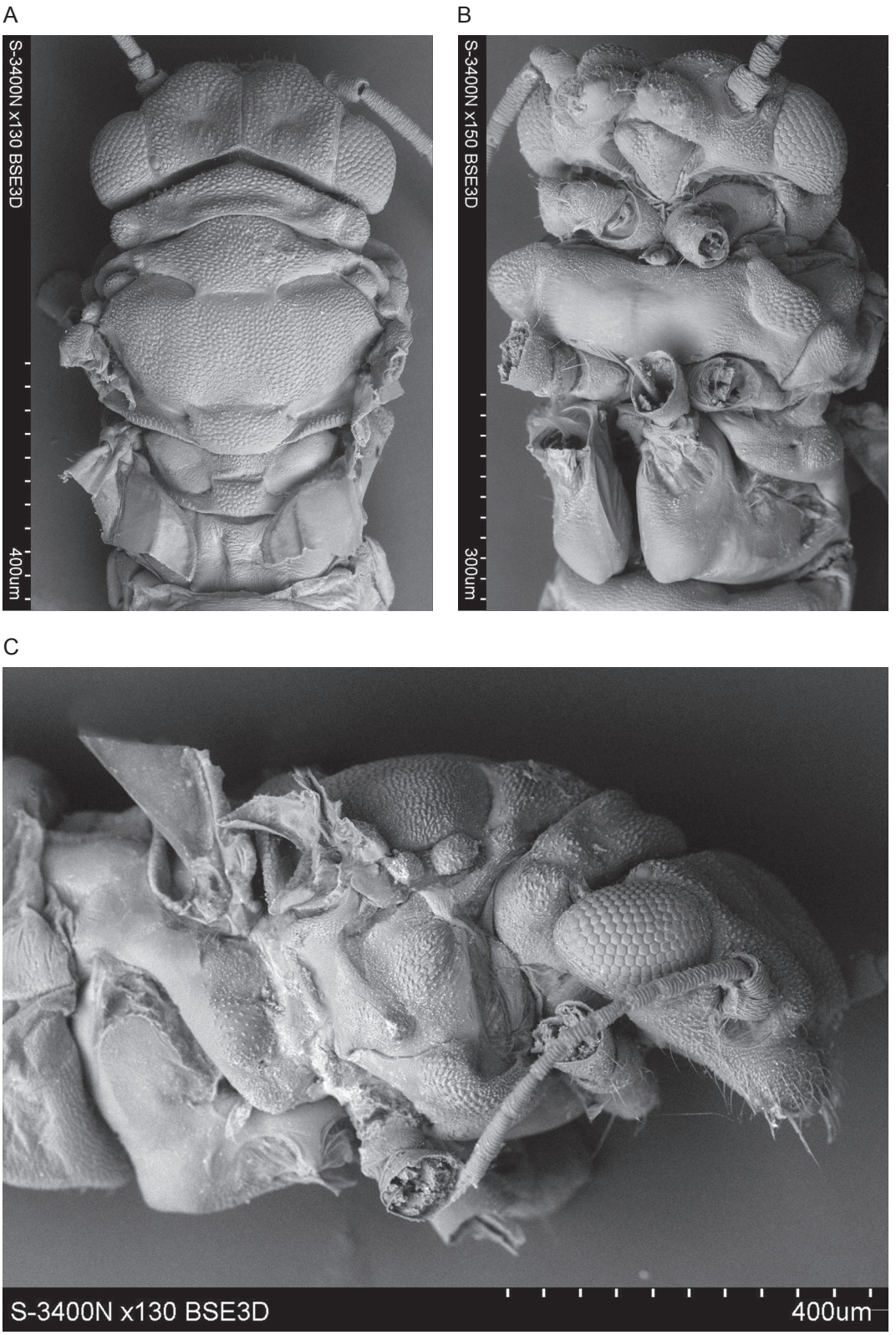


Fig. 15. *Blastopsylla occidentalis* Taylor, 1985; **A** – dorsal side, **B** – ventral side, **C** – lateral side

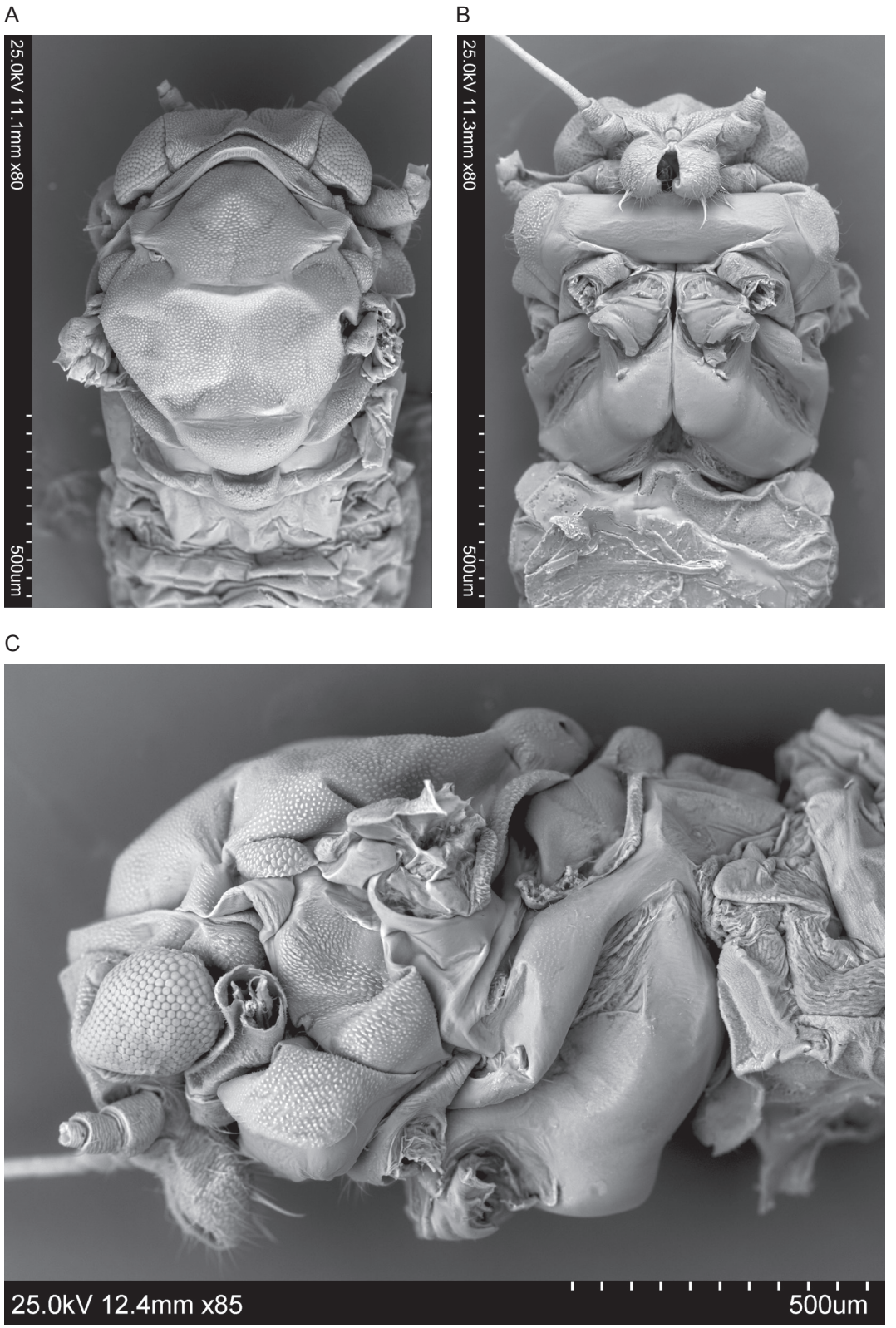


Fig. 16. *Creiis tecta* Maskell, 1898; **A** – dorsal side, **B** – ventral side, **C** – lateral side

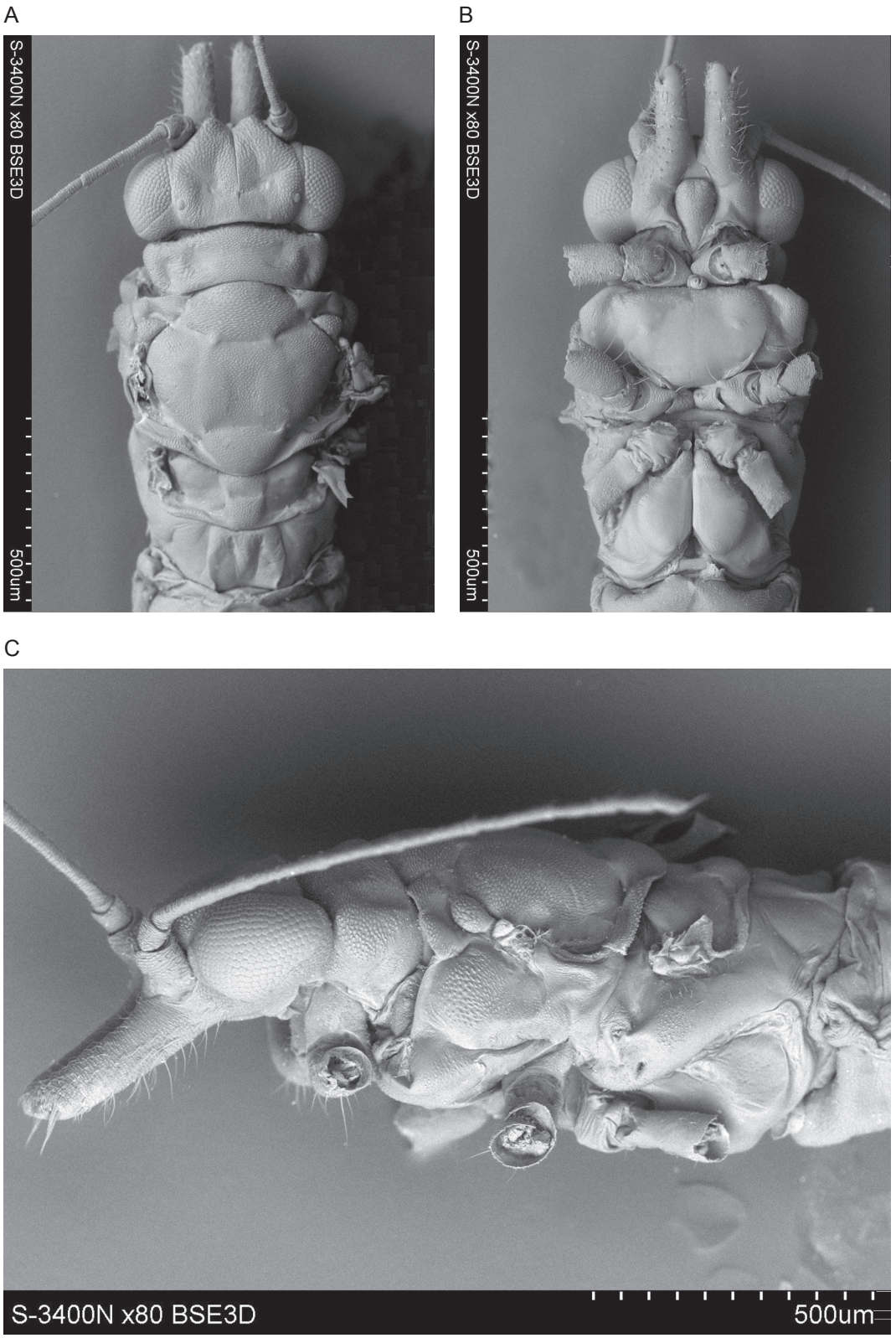


Fig. 17. *Glycaspis brimblecombei* Moore, 1964; **A** – dorsal side, **B** – ventral side, **C** – lateral side

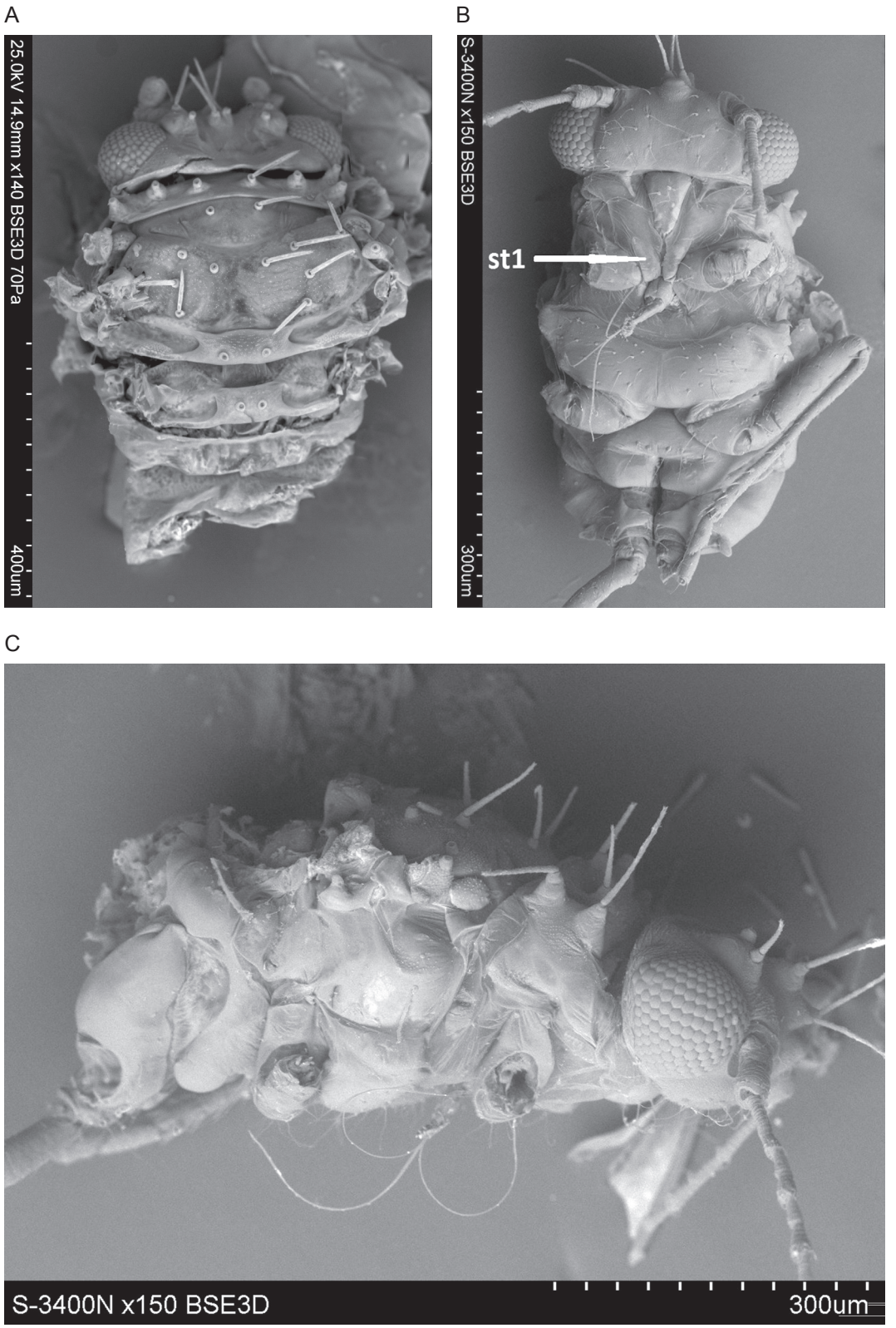


Fig. 18. *Togepsylla matsumurana* Kuwayama, 1949; **A** – dorsal side, **B** – ventral side, **C** – lateral side

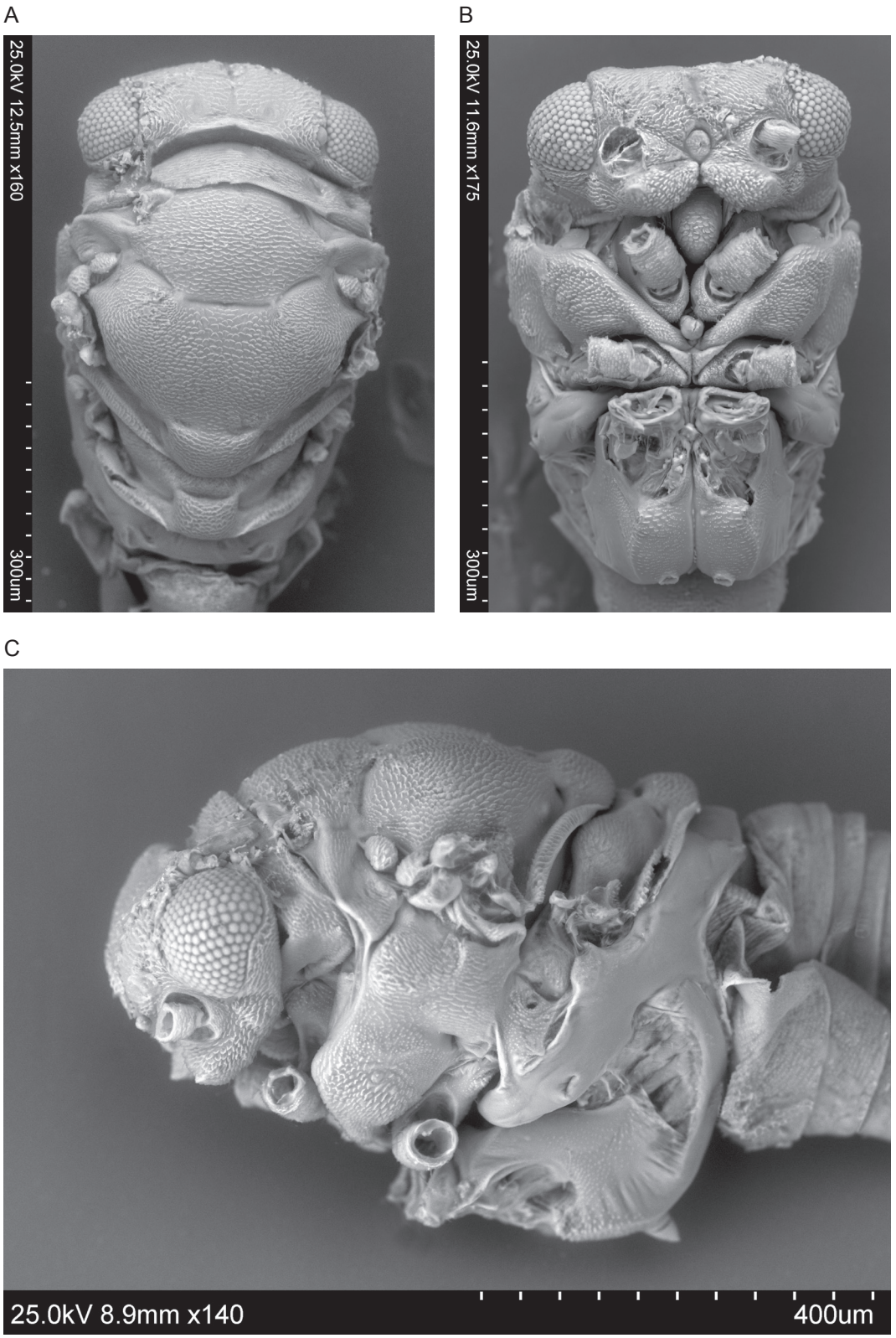


Fig. 19. *Calophya rhois* (Löw, 1877); **A** – dorsal side, **B** – ventral side, **C** – lateral side

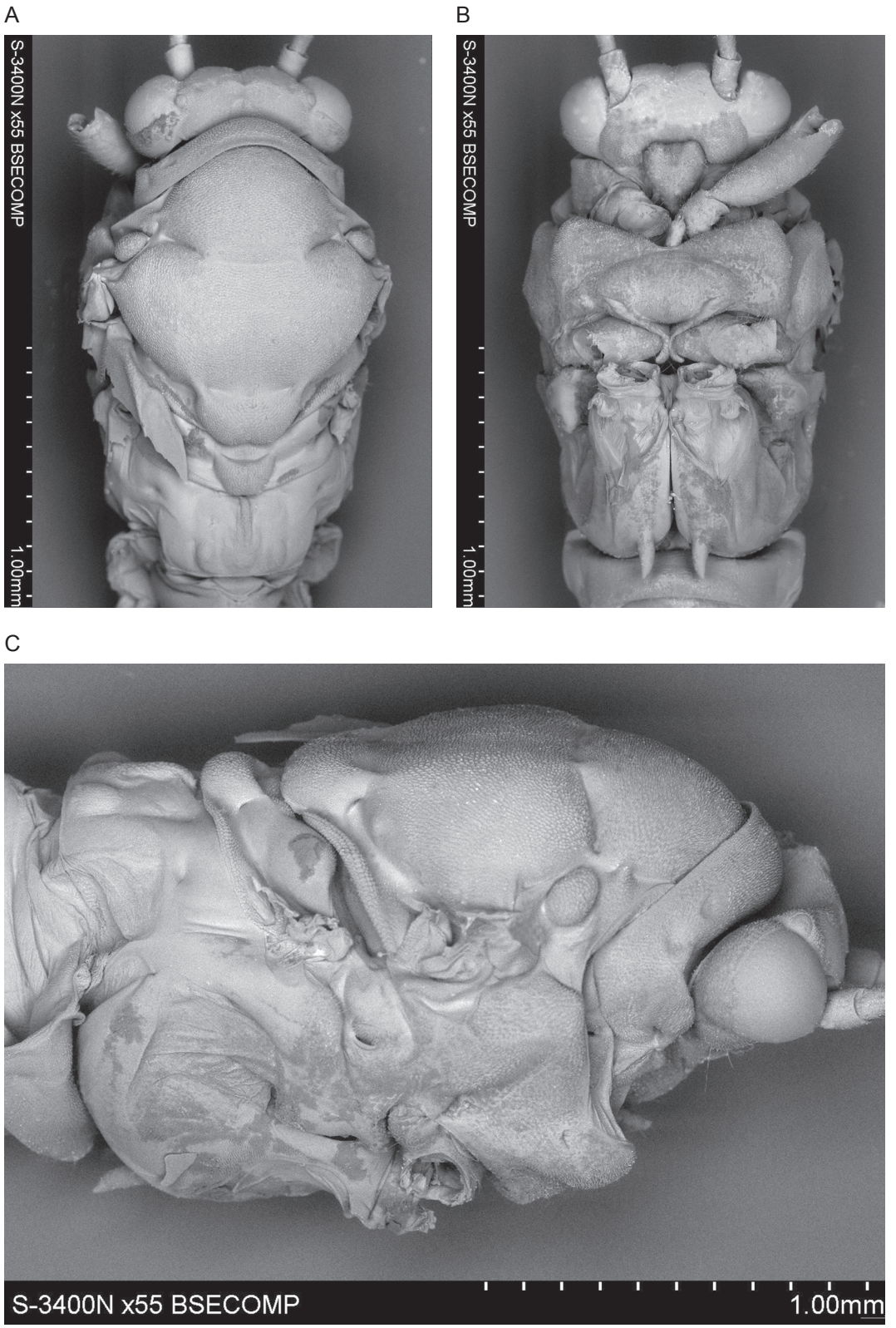


Fig. 20. *Bharatiana octospinosa* Mathur, 1973; **A** – dorsal side, **B** – ventral side, **C** – lateral side

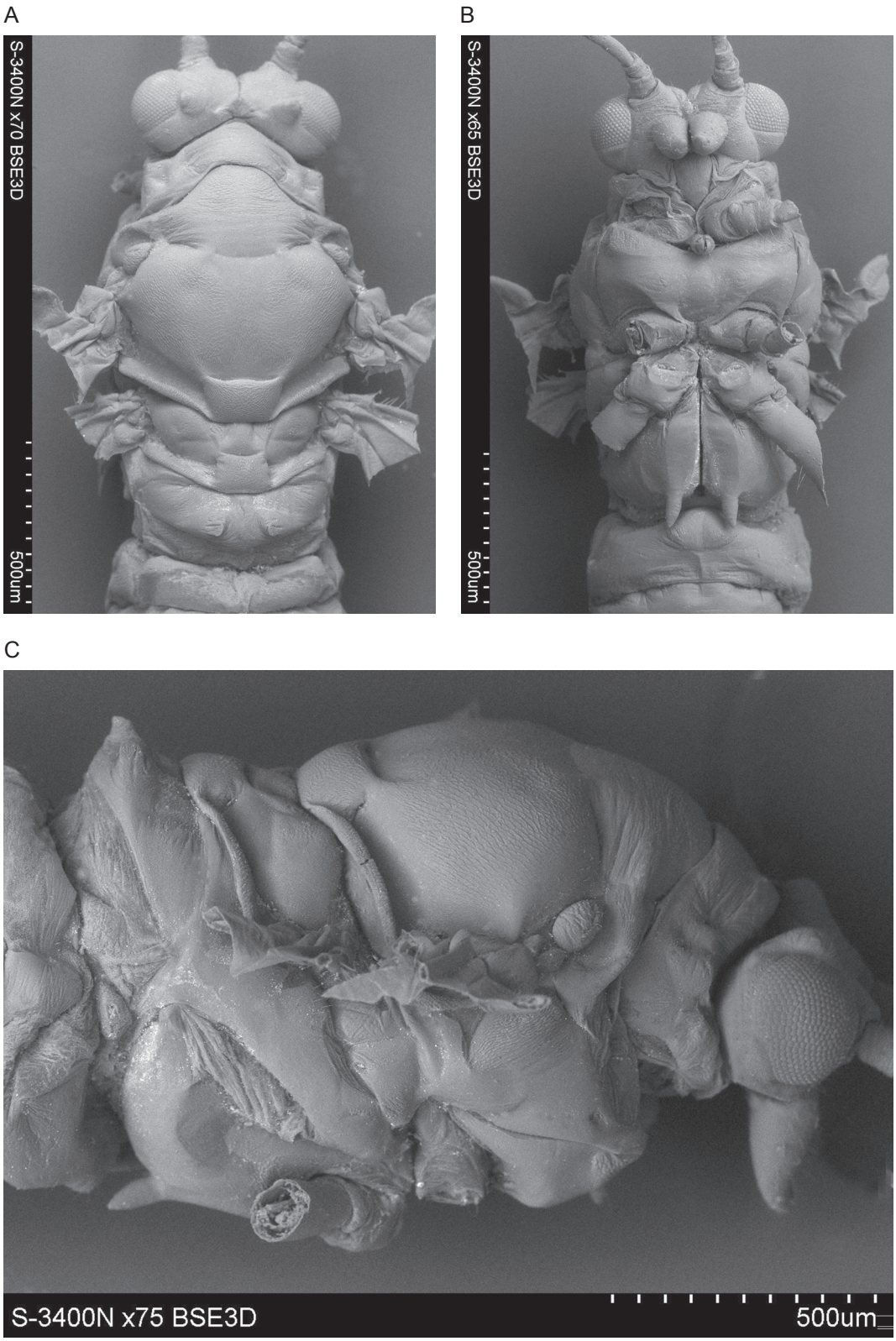


Fig. 21. *Cecidopsylla schimae* Kieffer, 1905; **A** – dorsal side, **B** – ventral side, **C** – lateral side

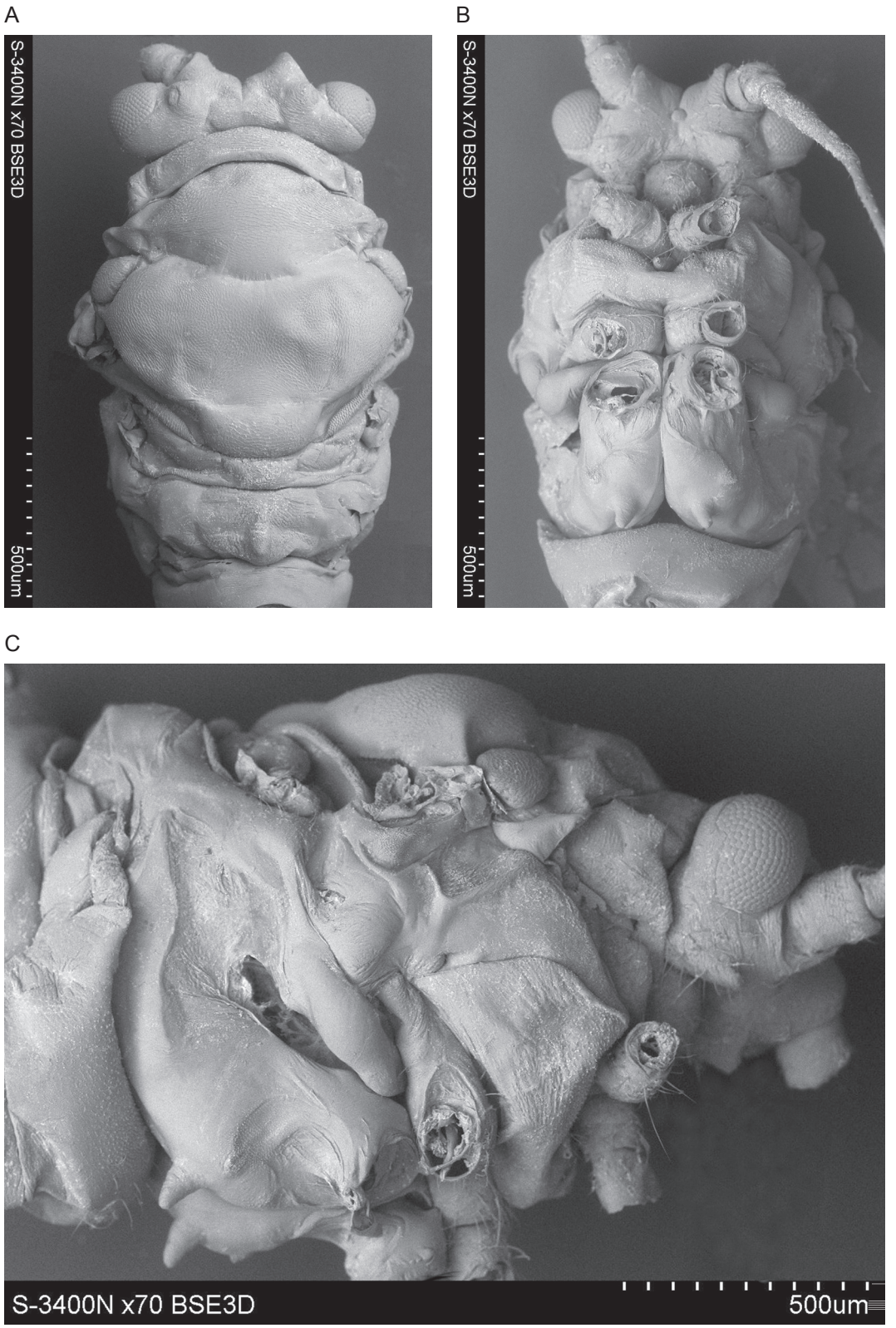


Fig. 22. *Mastigimas reseri* Burckhardt, Queiroz and Drohojowska, 2013; **A** – dorsal side, **B** – ventral side, **C** – lateral side

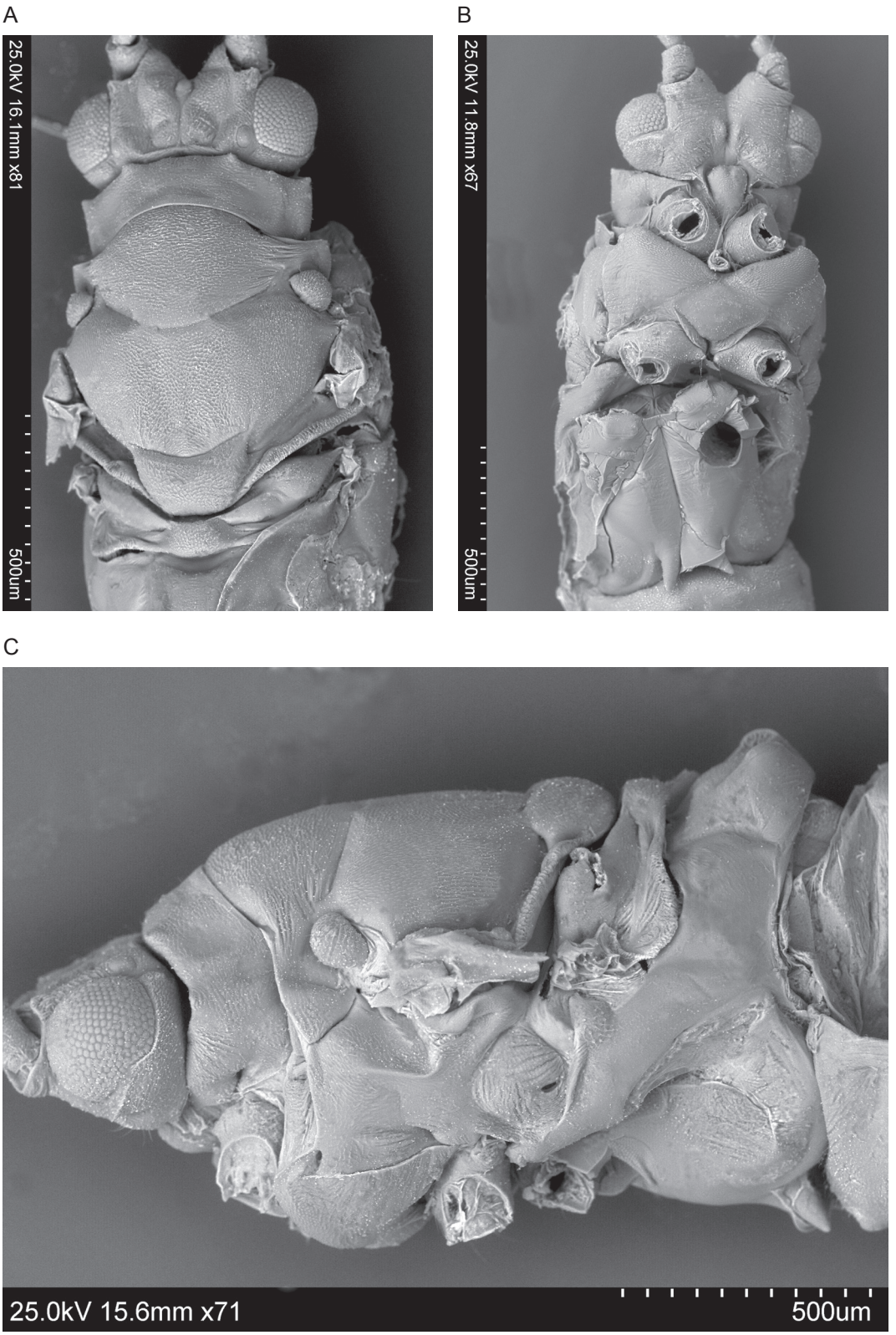


Fig. 23. *Mesohomotoma lineaticollis* Enderlein, 1914; **A** – dorsal side, **B** – ventral side, **C** – lateral side

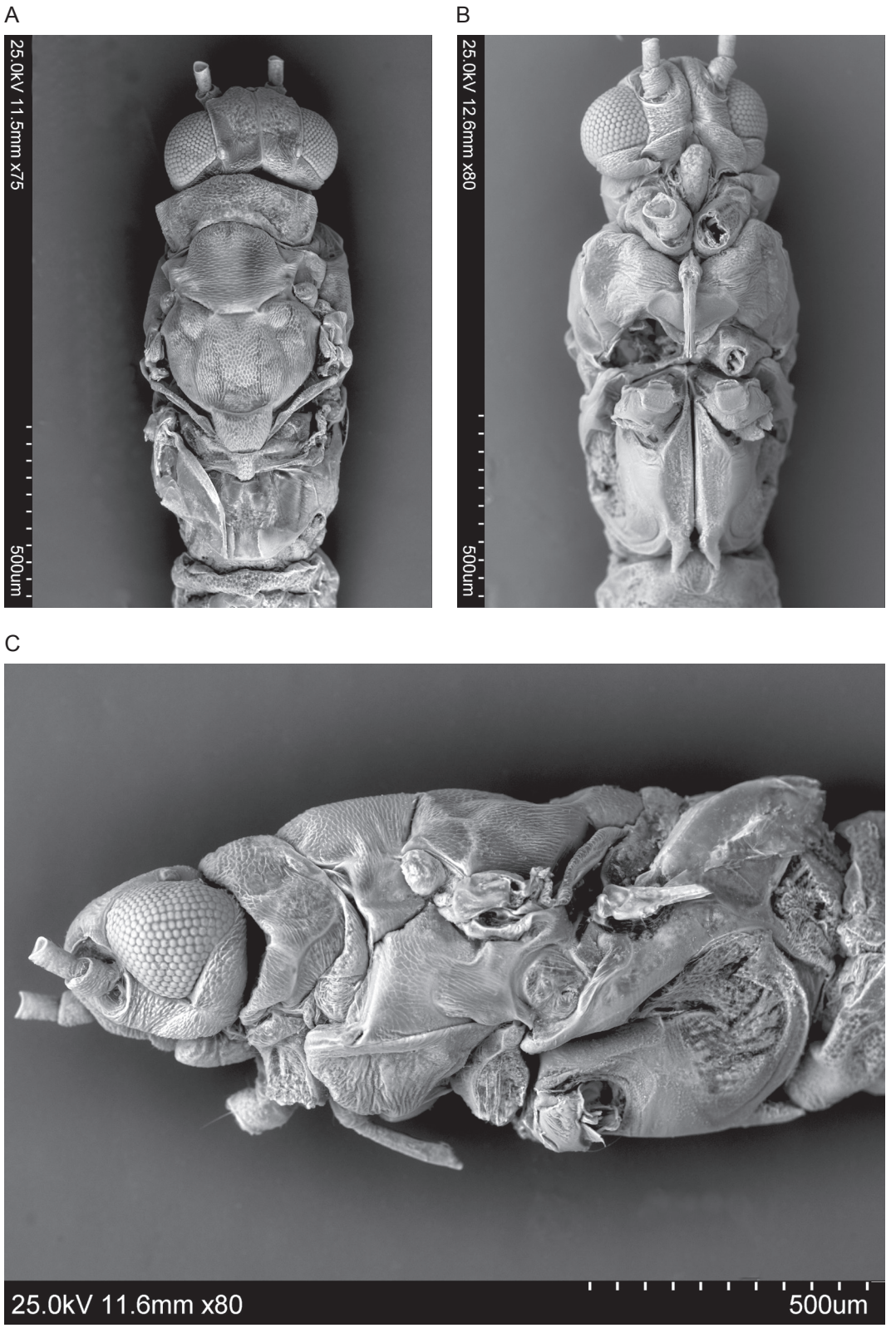


Fig. 24. *Tenaphalara acutipennis* Kuwayama, 1908; **A** – dorsal side, **B** – ventral side, **C** – lateral side

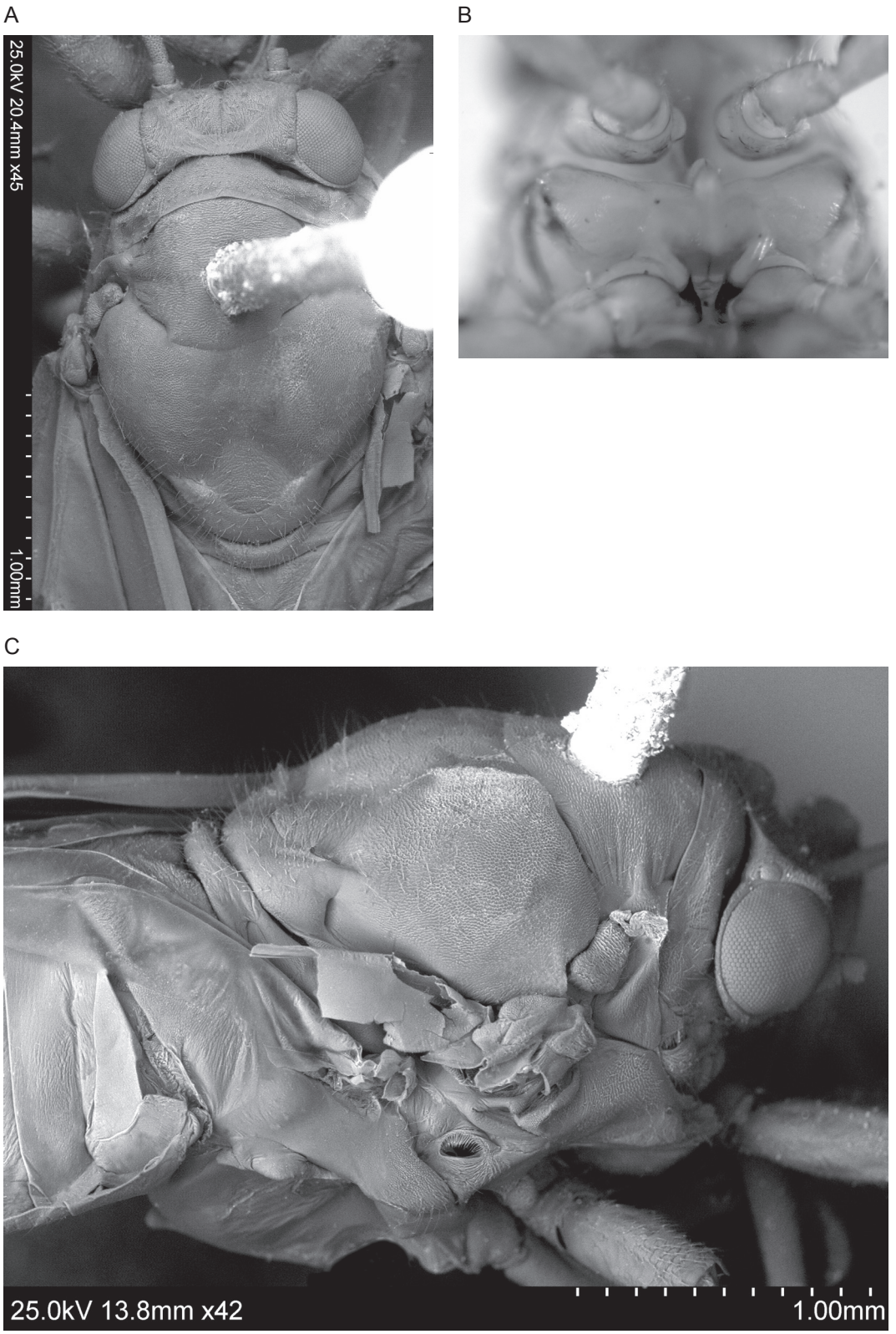


Fig. 25. *Triozamia lamborni* (Newstead, 1914); **A** – dorsal side, **B** – ventral side of mesothorax, electron microscope photo, **C** – lateral side

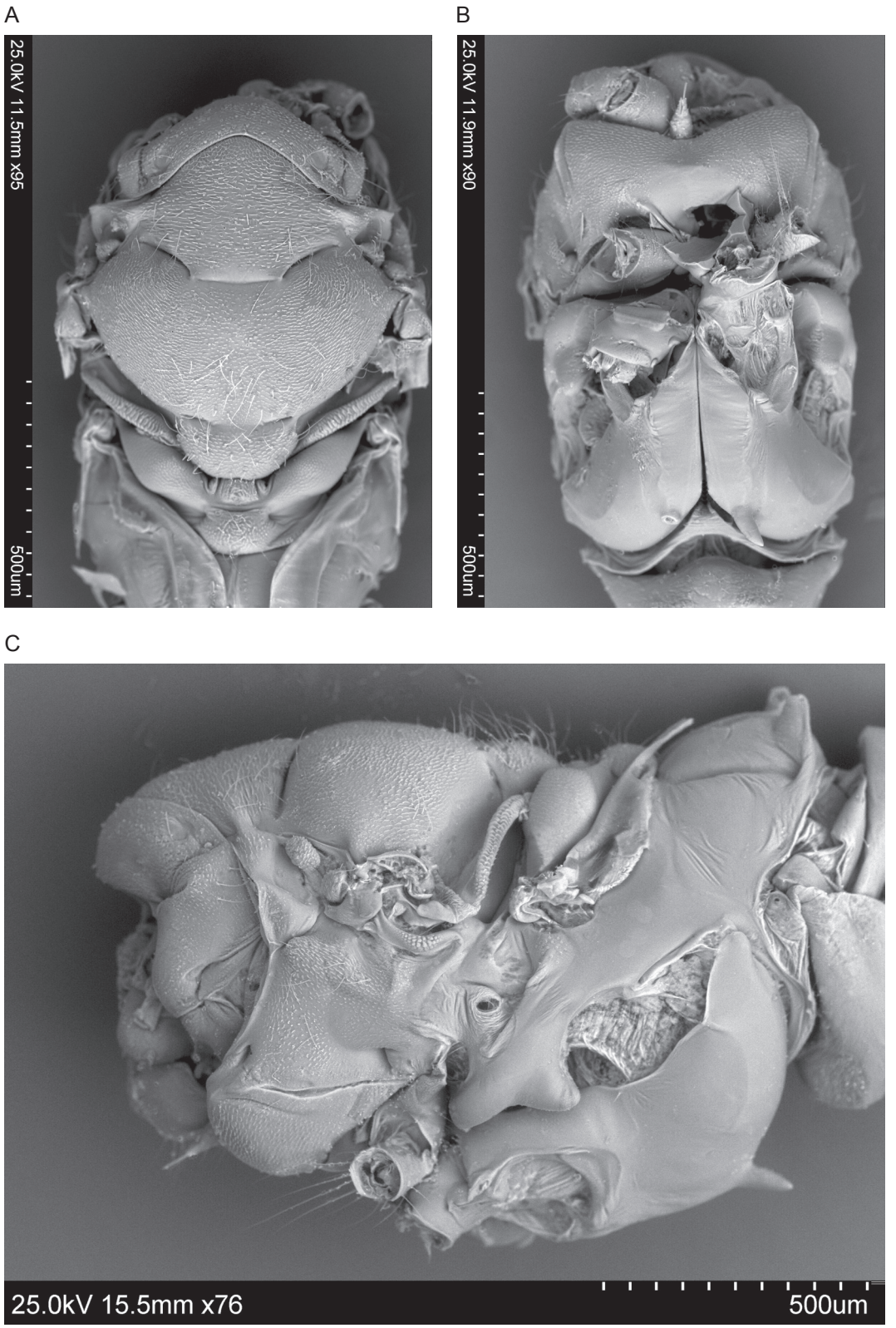


Fig. 26. *Homotoma ficus* (Linnaeus, 1758); 24 **A** – dorsal side, **B** – ventral side, **C** – lateral side

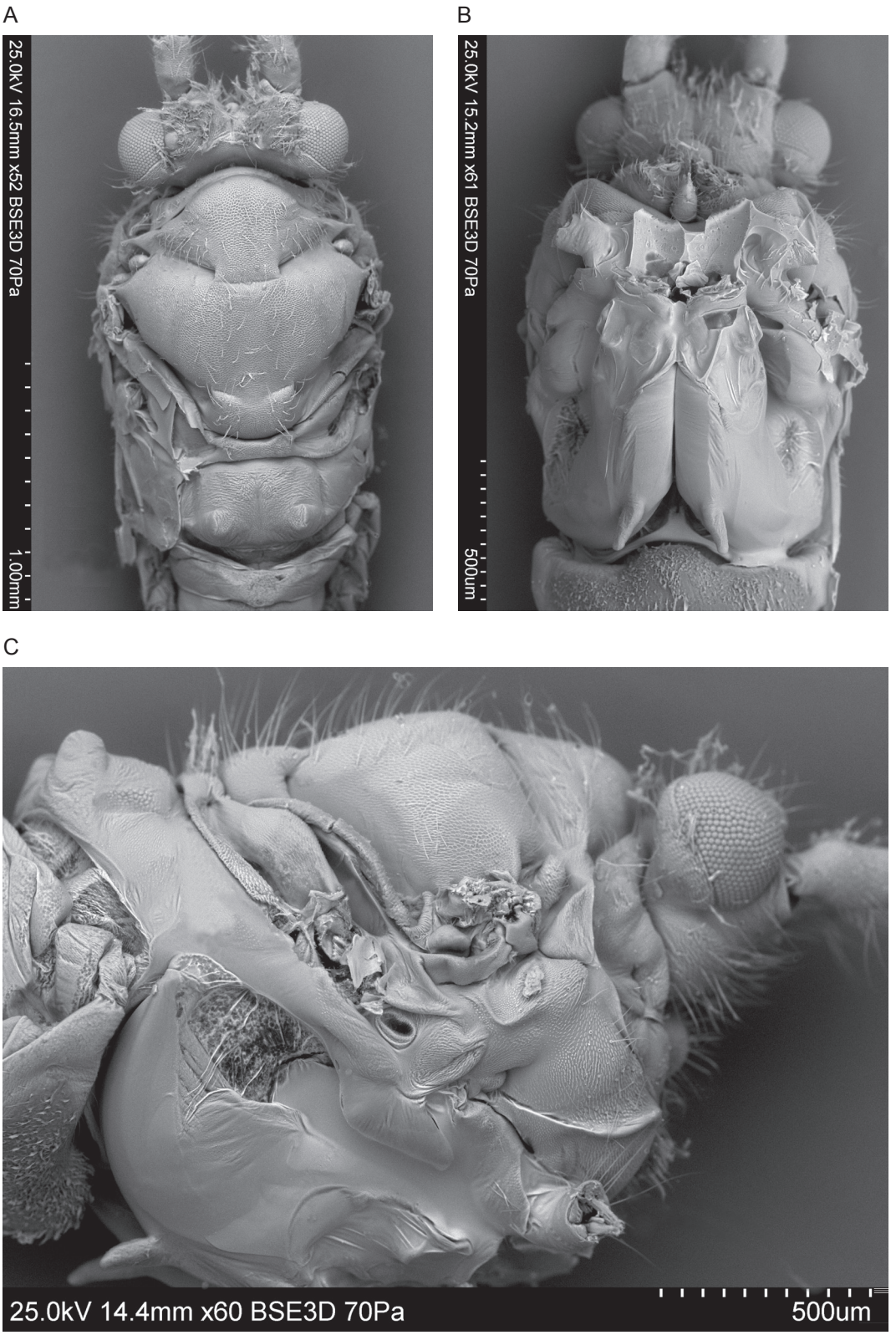


Fig. 27. *Mycopsylla fici* (Tryon, 1895); **A** – dorsal side, **B** – ventral side, **C** – lateral side

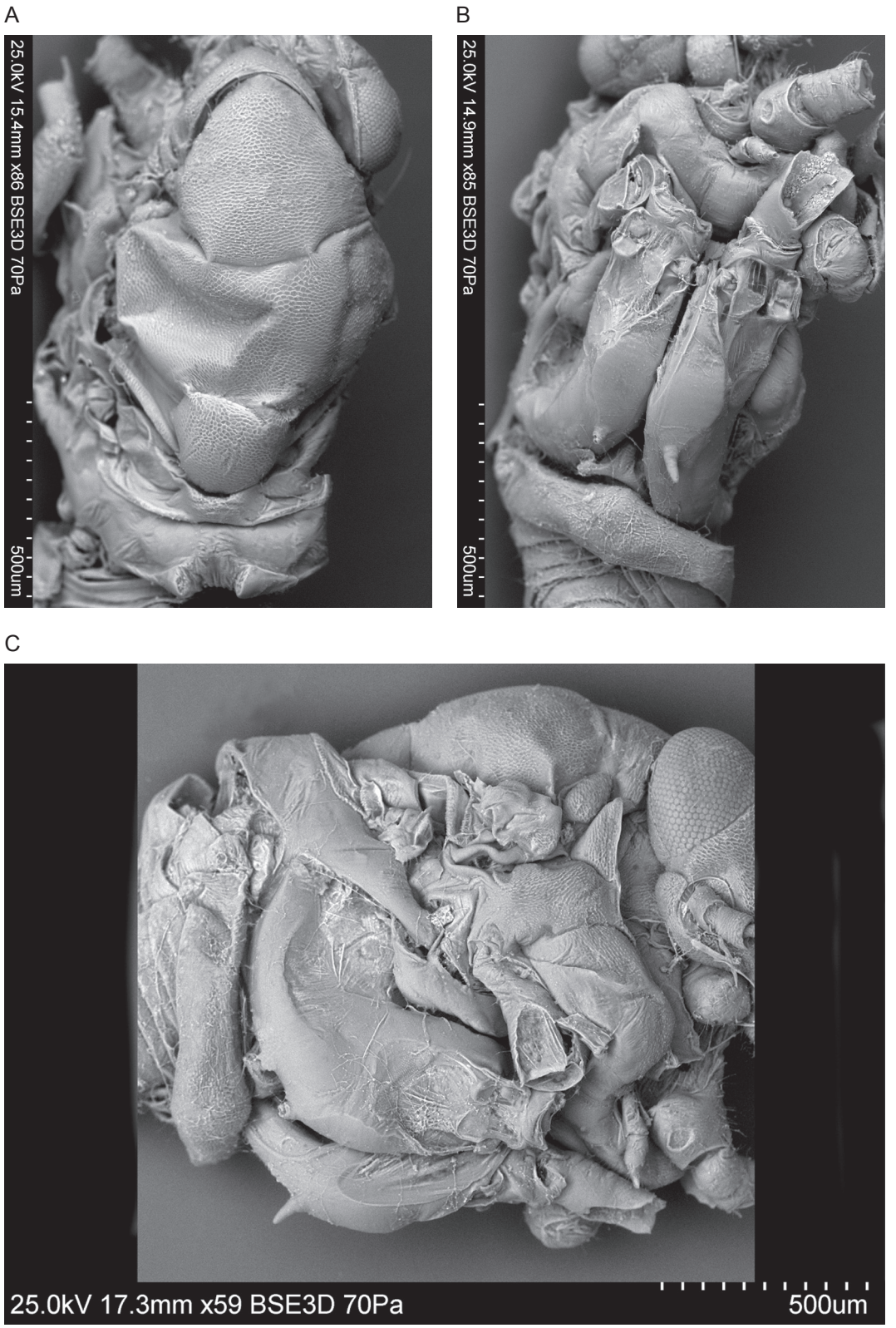


Fig. 28. *Macrohomotoma gladiata* Kuwayama, 1908; **A** – dorsal side, **B** – ventral side, **C** – lateral side

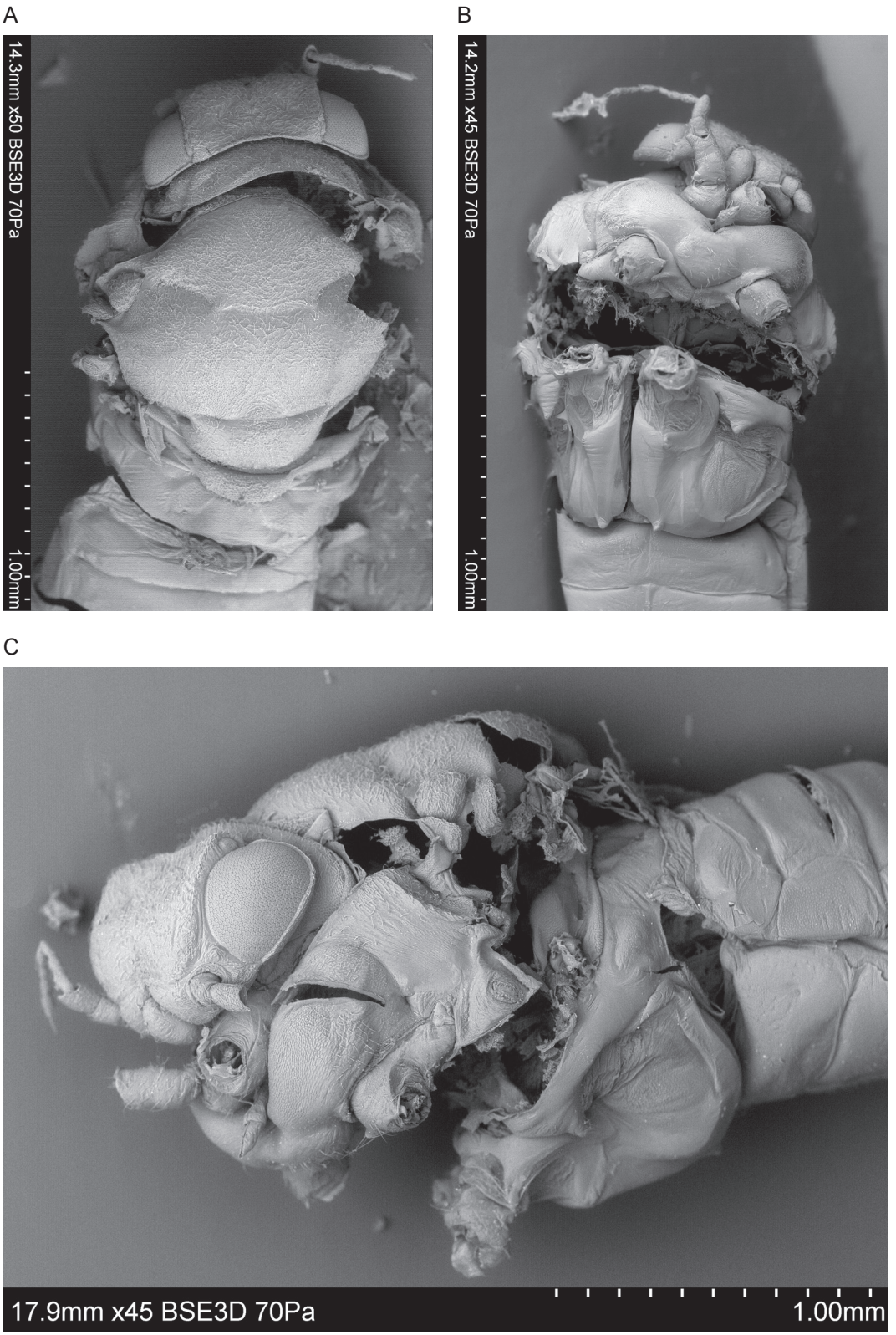


Fig. 29. *Phytolyma fusca* Alibert, 1947; **A** – dorsal side, **B** – ventral side, **C** – lateral side

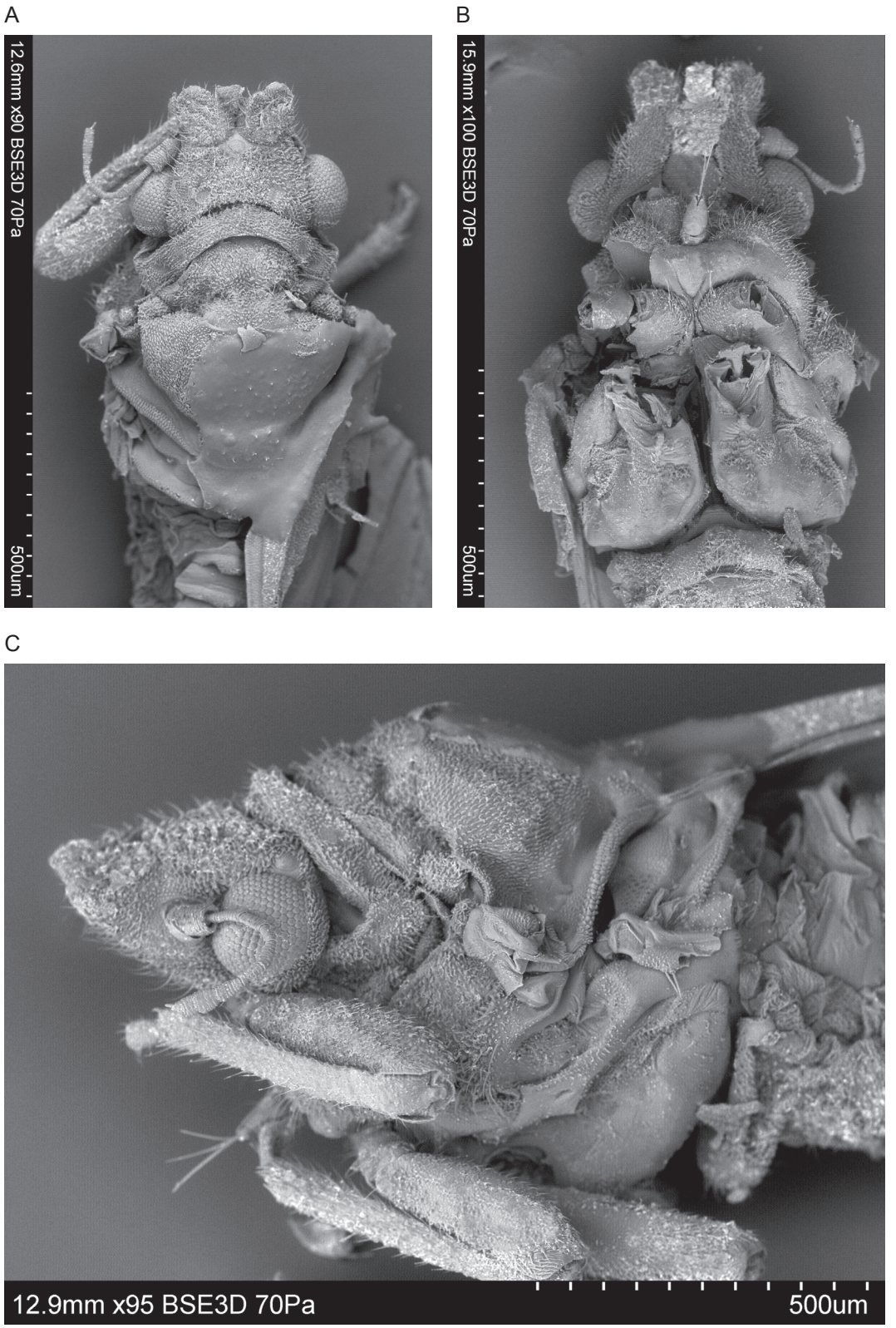


Fig. 30. *Diaphorina truncata* Crawford, 1924; **A** – dorsal side, **B** – ventral side, **C** – lateral side

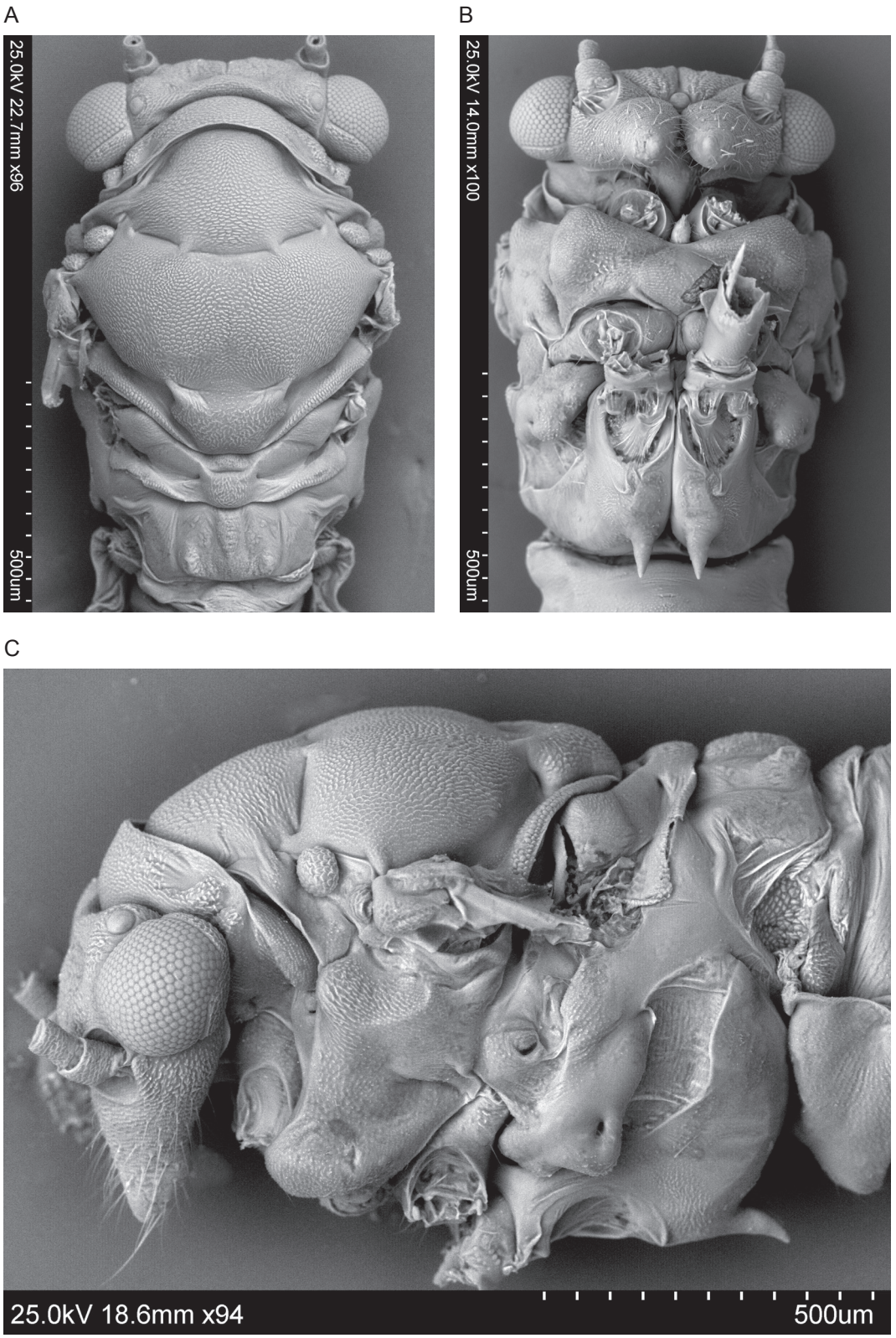


Fig. 31. *Psyllopsis fraxinicola* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side

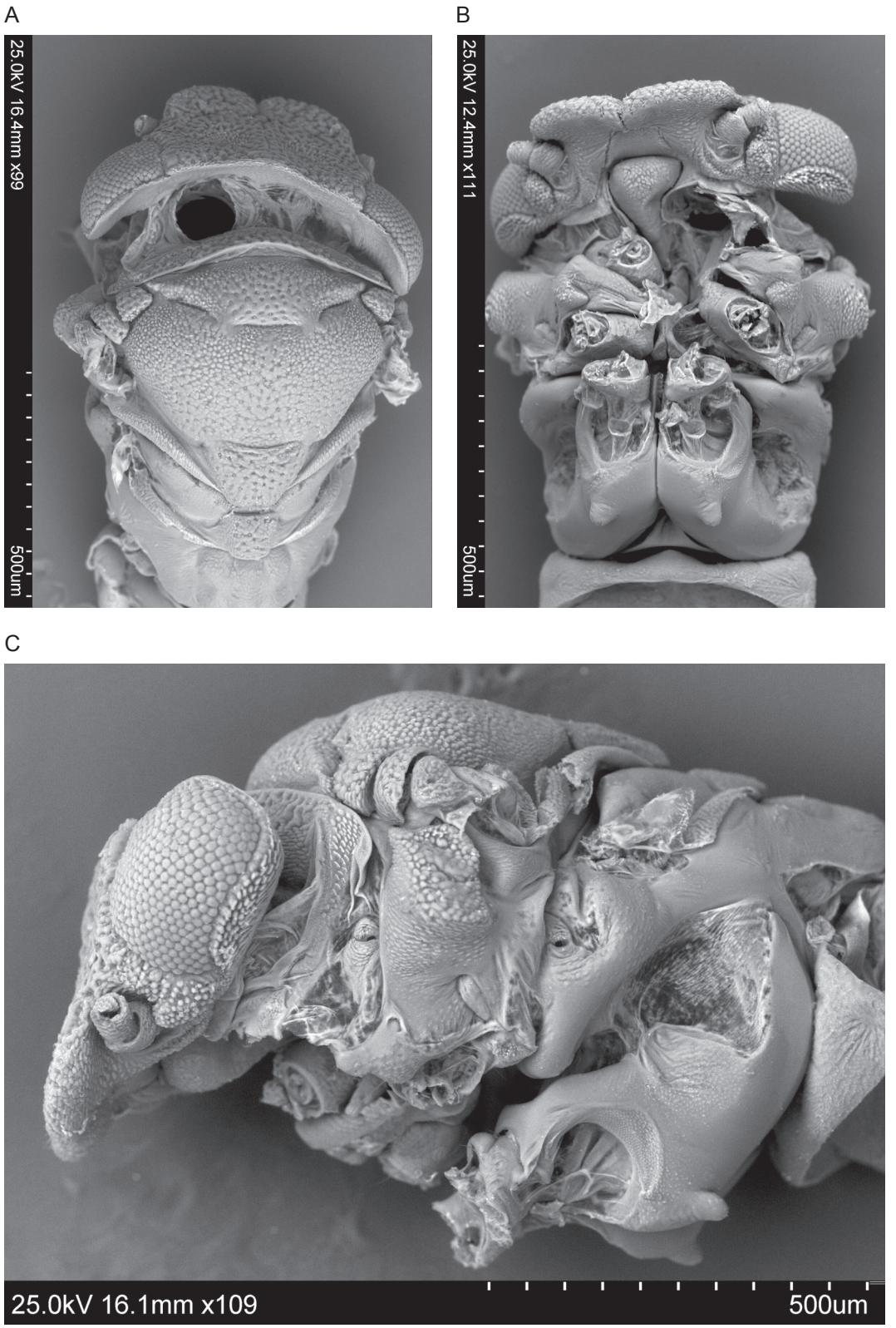


Fig. 32. *Euphyllura olivina* (Costa, 1839); **A** – dorsal side, **B** – ventral side, **C** – lateral side

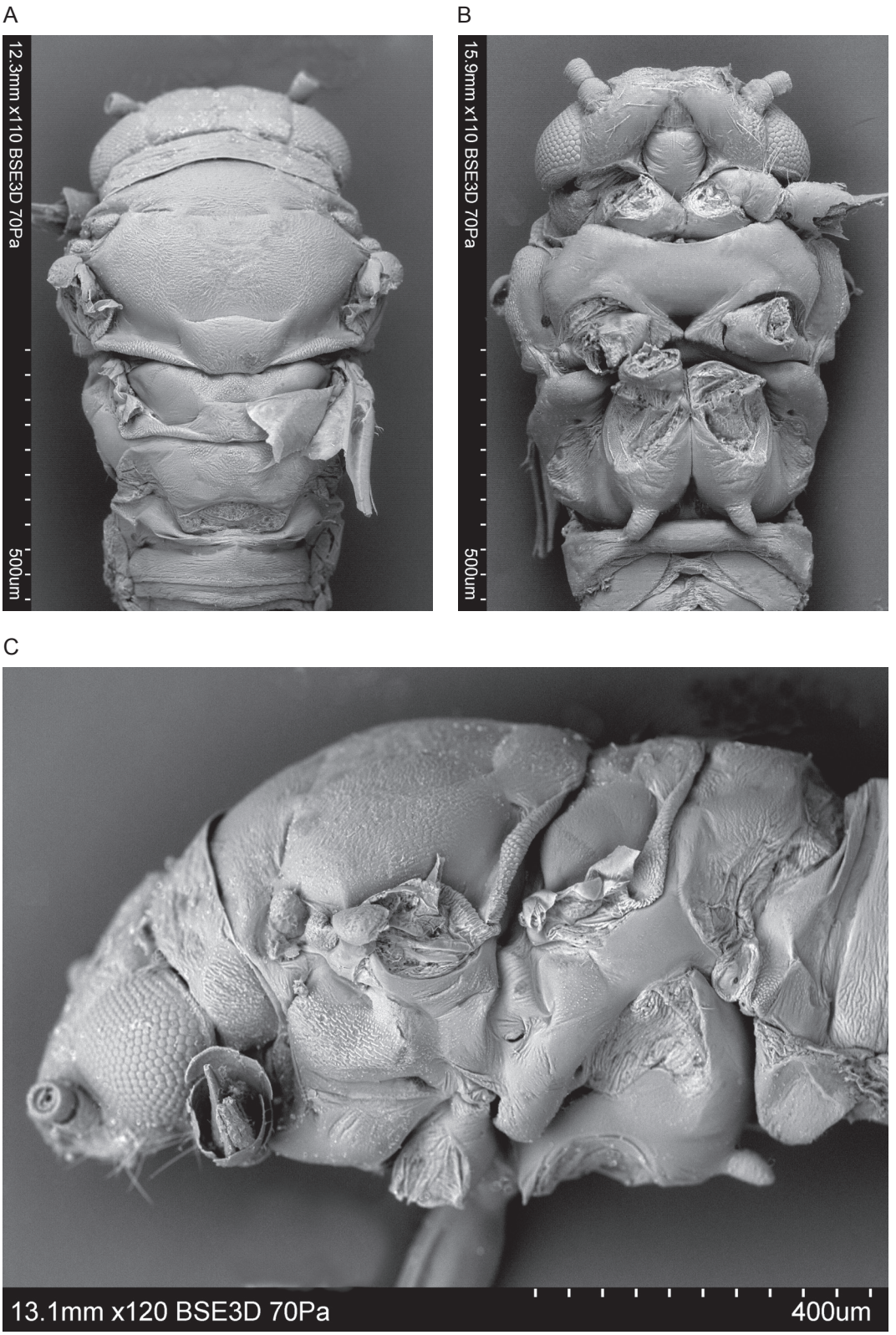


Fig. 33. *Pachypsylloides reverendus* Loginova, 1970; **A** – dorsal side, **B** – ventral side, **C** – lateral side

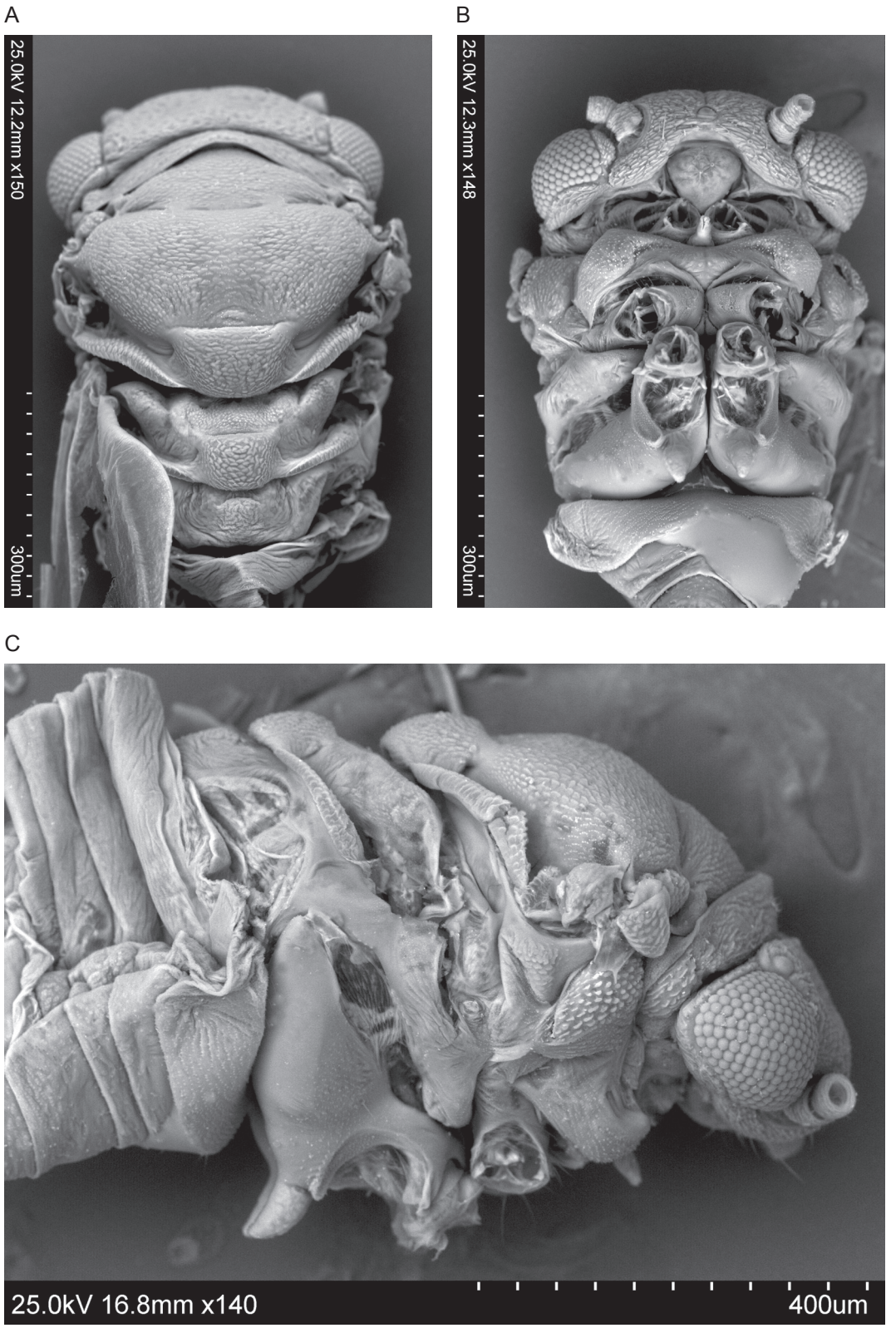


Fig. 34. *Strophingia cinereae* Hodkinson, 1971; **A** – dorsal side, **B** – ventral side, **C** – lateral side

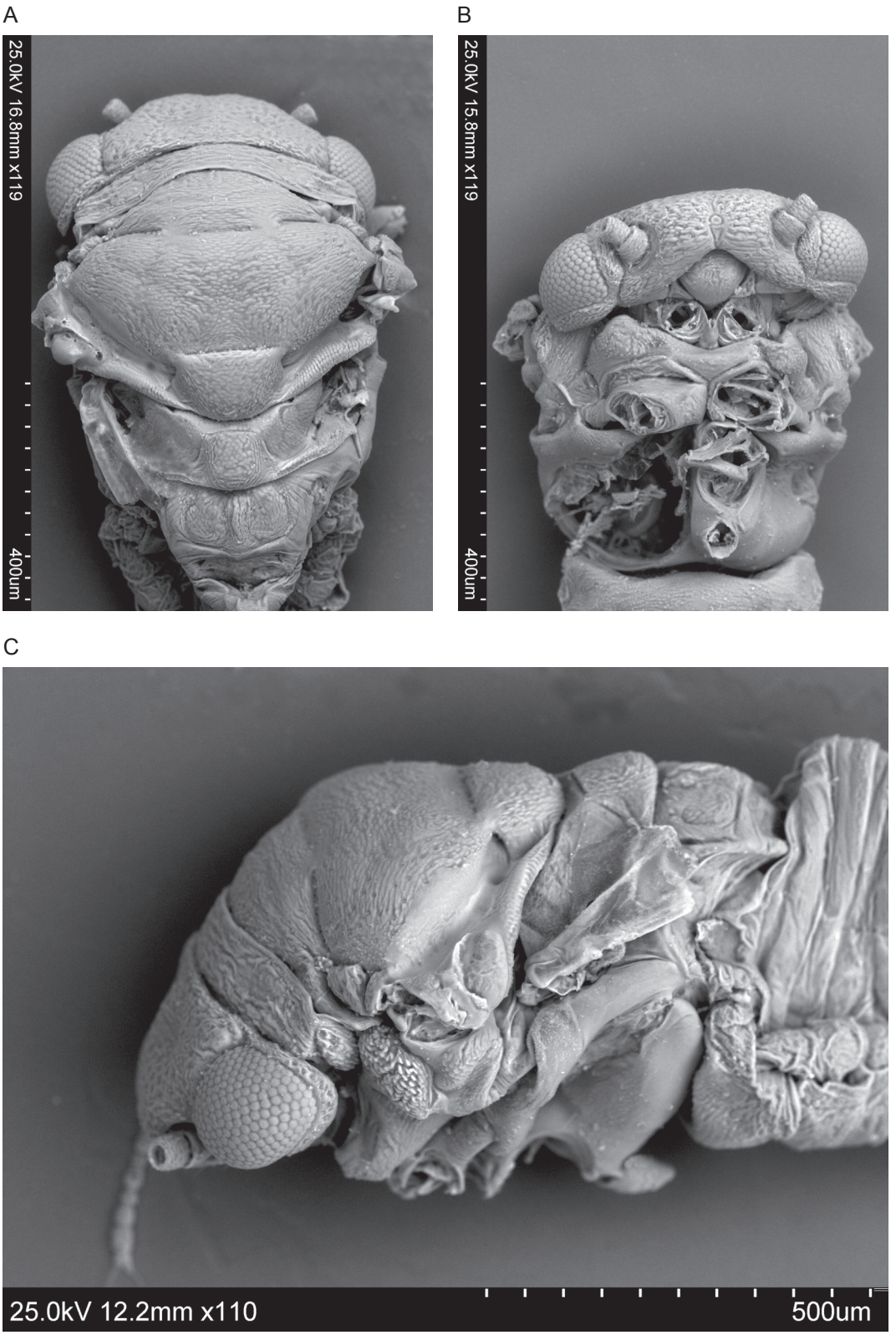


Fig. 35. *Strophingia proxima* Hodkinson, 1981; **A** – dorsal side, **B** – ventral side, **C** – lateral side

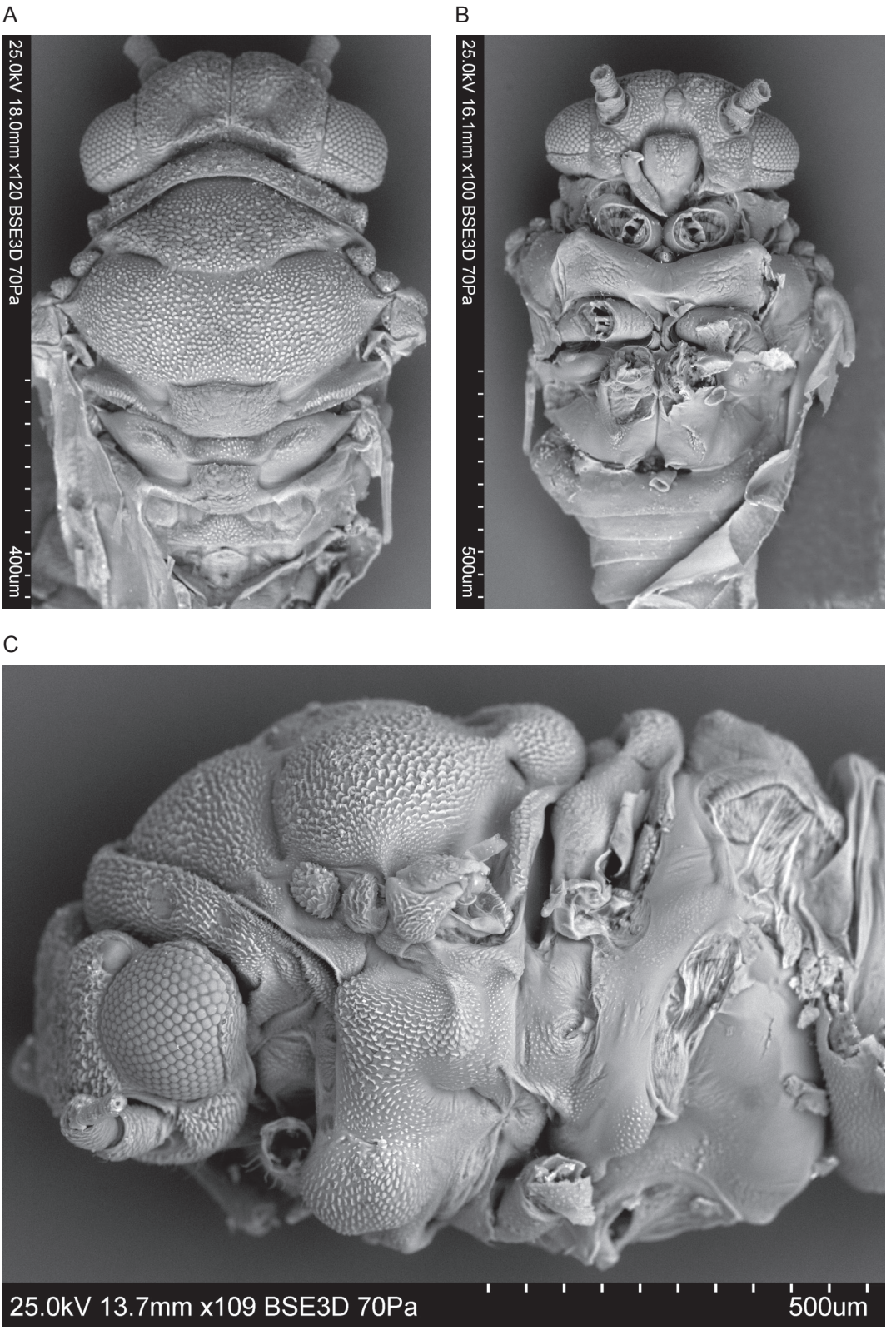


Fig. 36. *Camaratoscena speciosa* (Flor, 1861); **A** – dorsal side, **B** – ventral side, **C** – lateral side

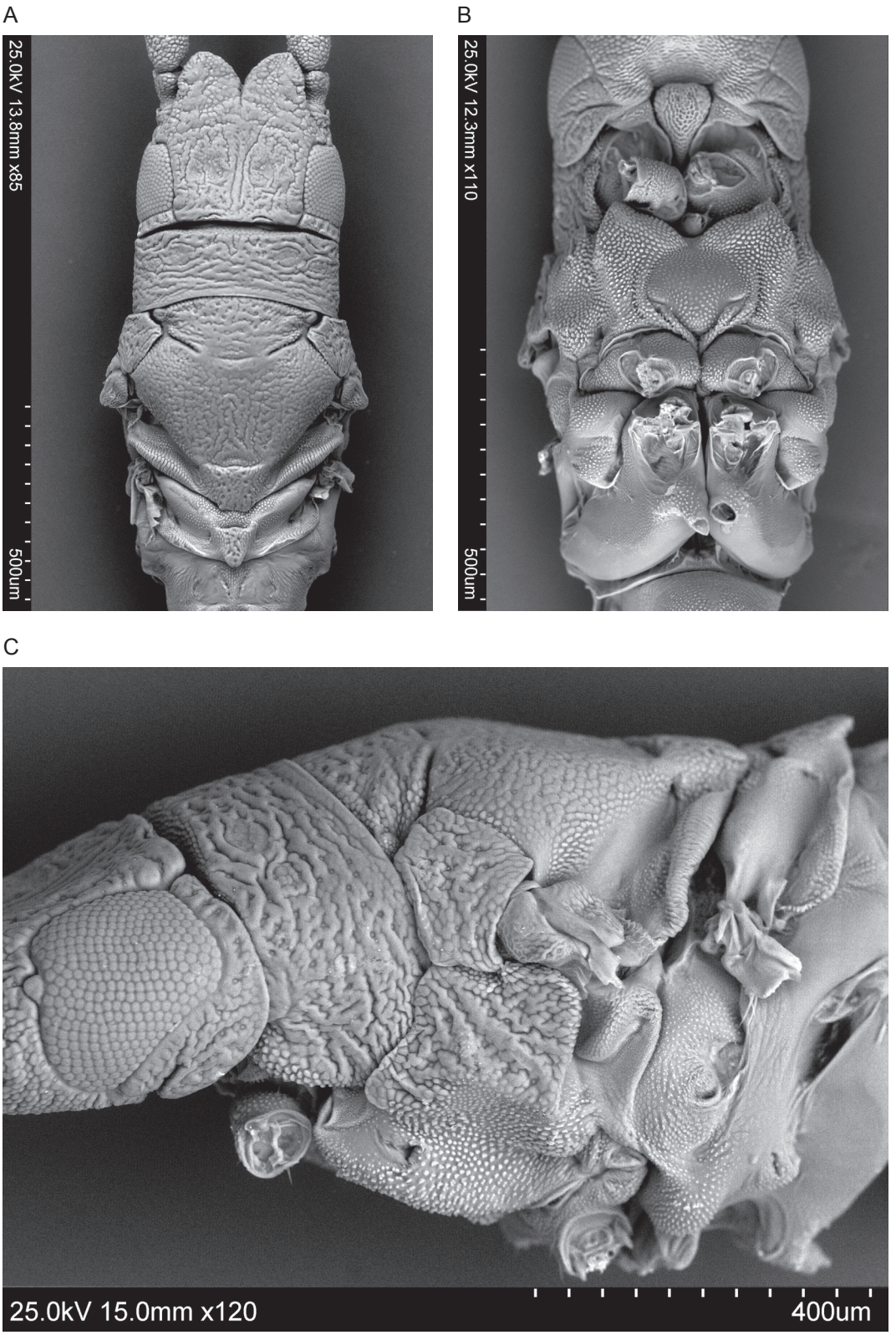


Fig. 37. *Livia junci* (Schrank, 1798); **A** – dorsal side, **B** – ventral side, **C** – lateral side (after Drohojowska 2009b)

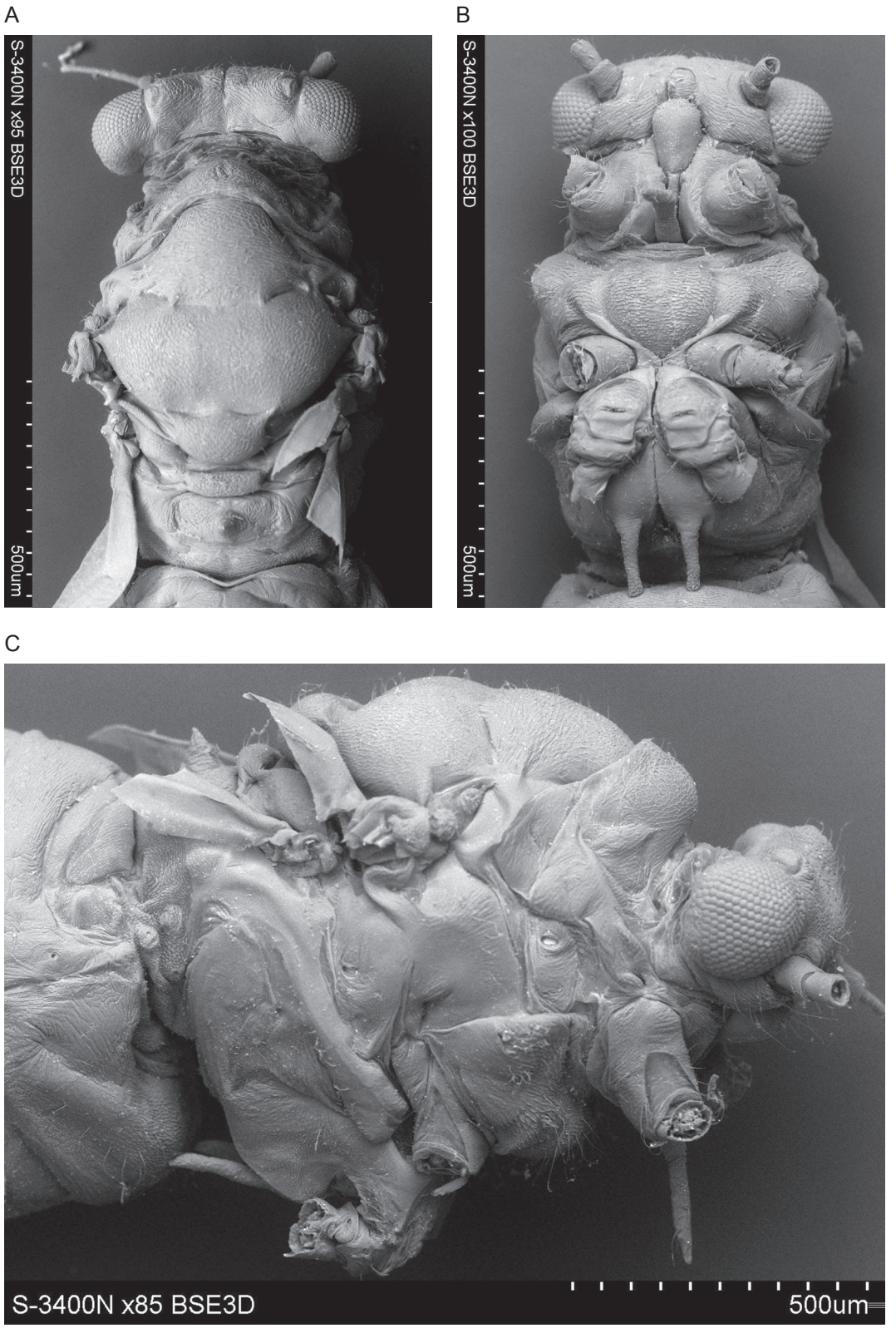


Fig. 38. *Paurocephala psylloptera* Crawford, 1913; **A** – dorsal side, **B** – ventral side, **C** – lateral side

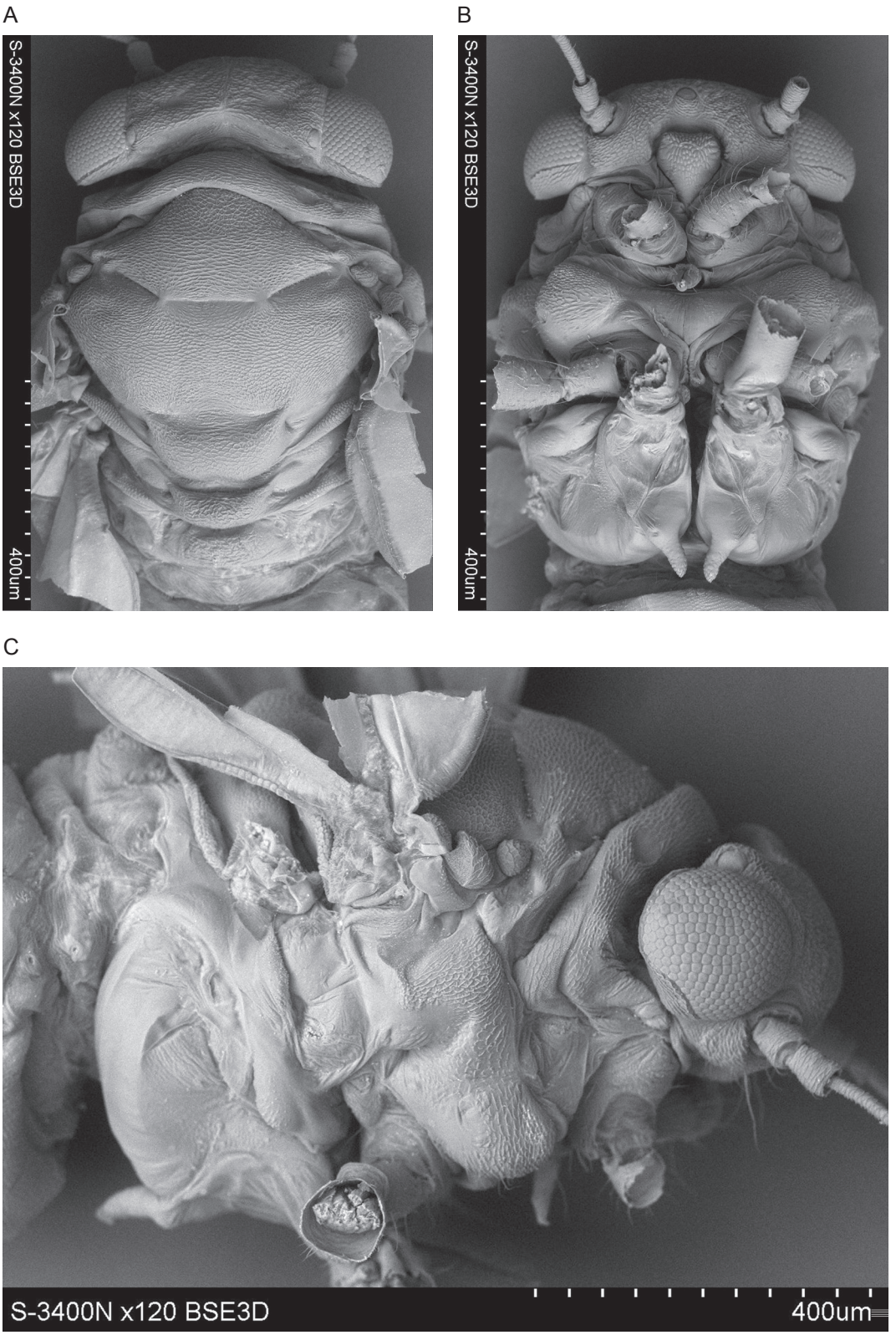


Fig. 39. *Syntomoza unicolor* (Loginova, 1958); **A** – dorsal side, **B** – ventral side, **C** – lateral side

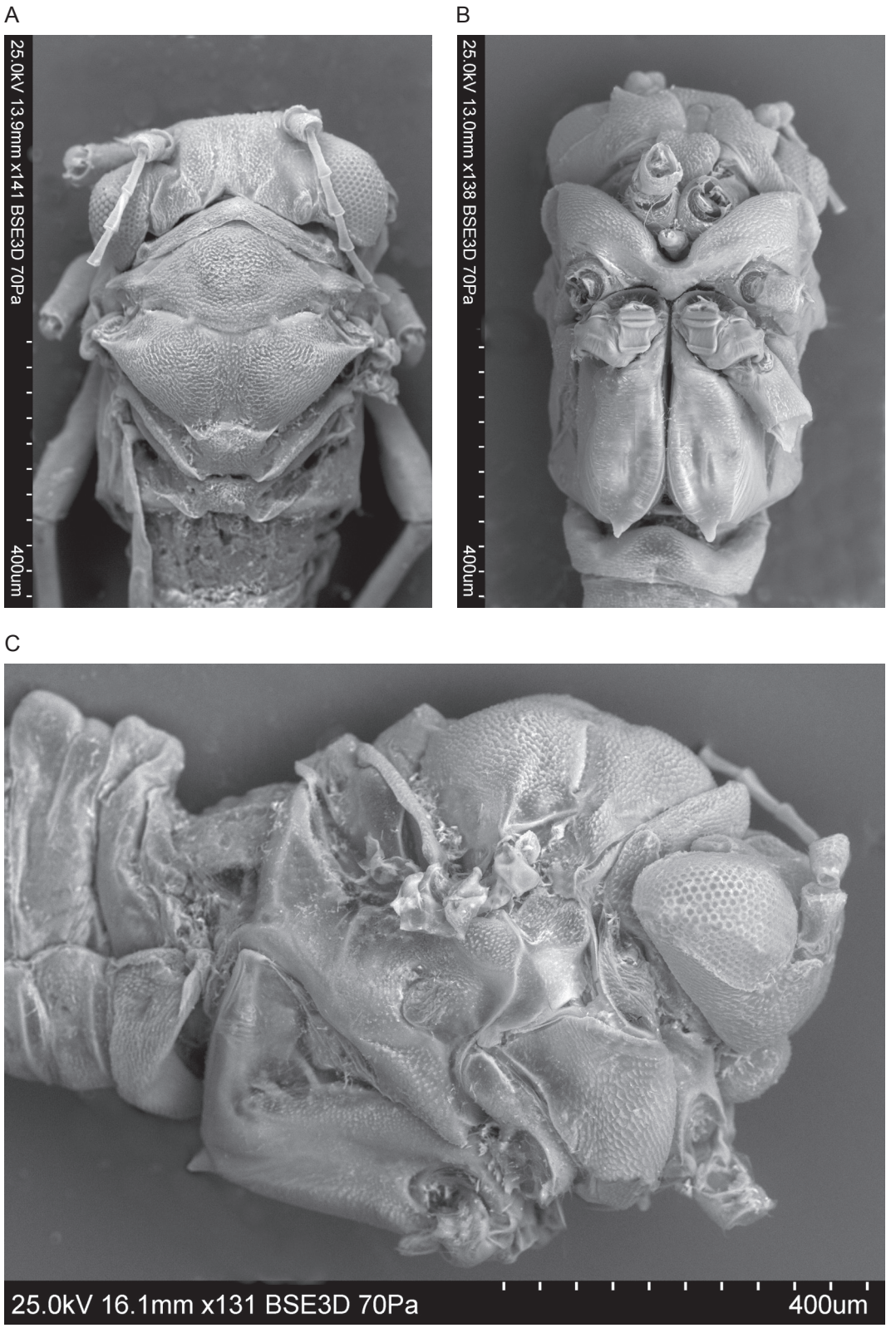


Fig. 40. *Pseudophacopteron zimmermanni* (Aulmann, 1912); **A** – dorsal side, **B** – ventral side, **C** – lateral side

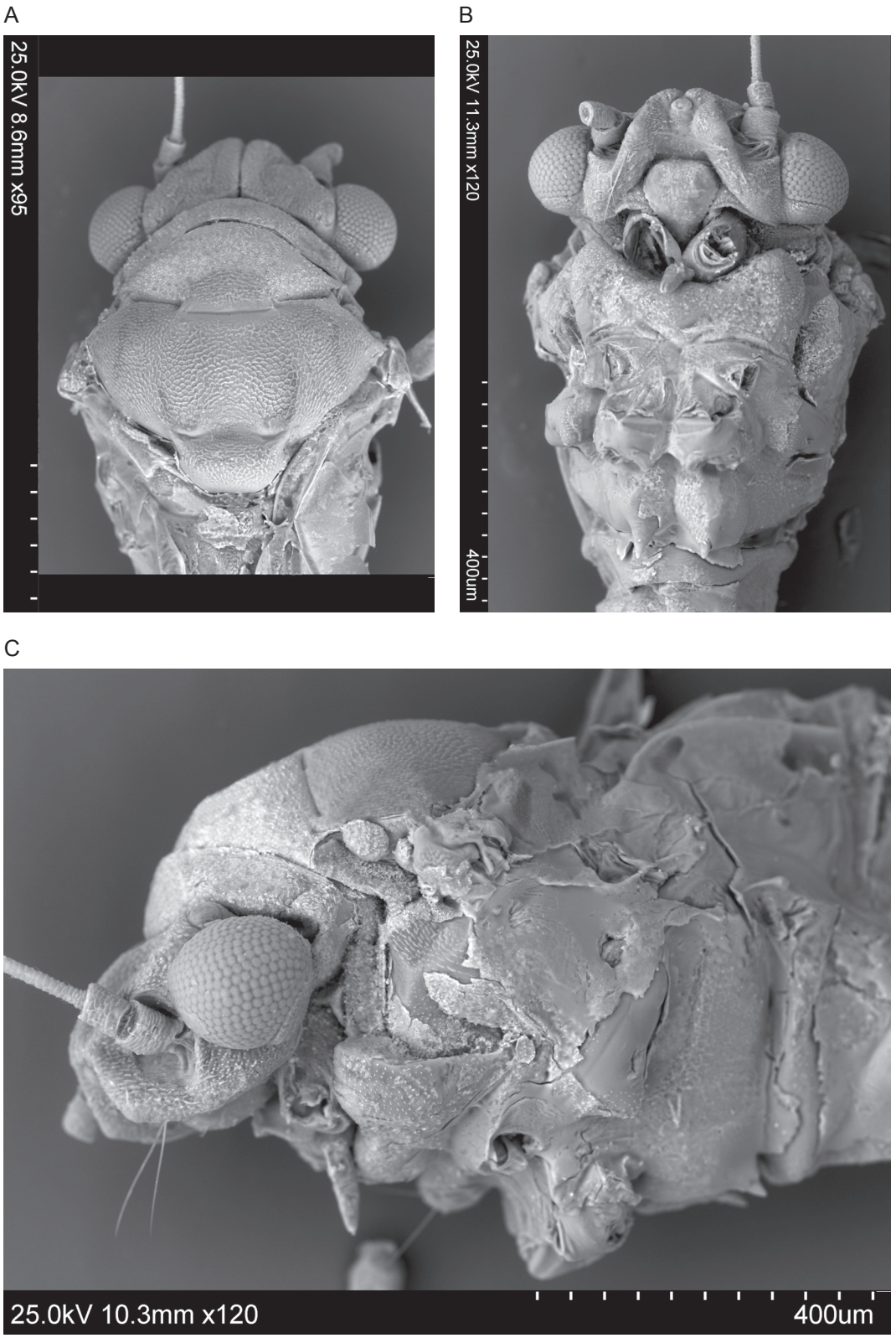


Fig. 41. *Acizzia hollisi* Burckhardt, 1981; **A** – dorsal side, **B** – ventral side, **C** – lateral side

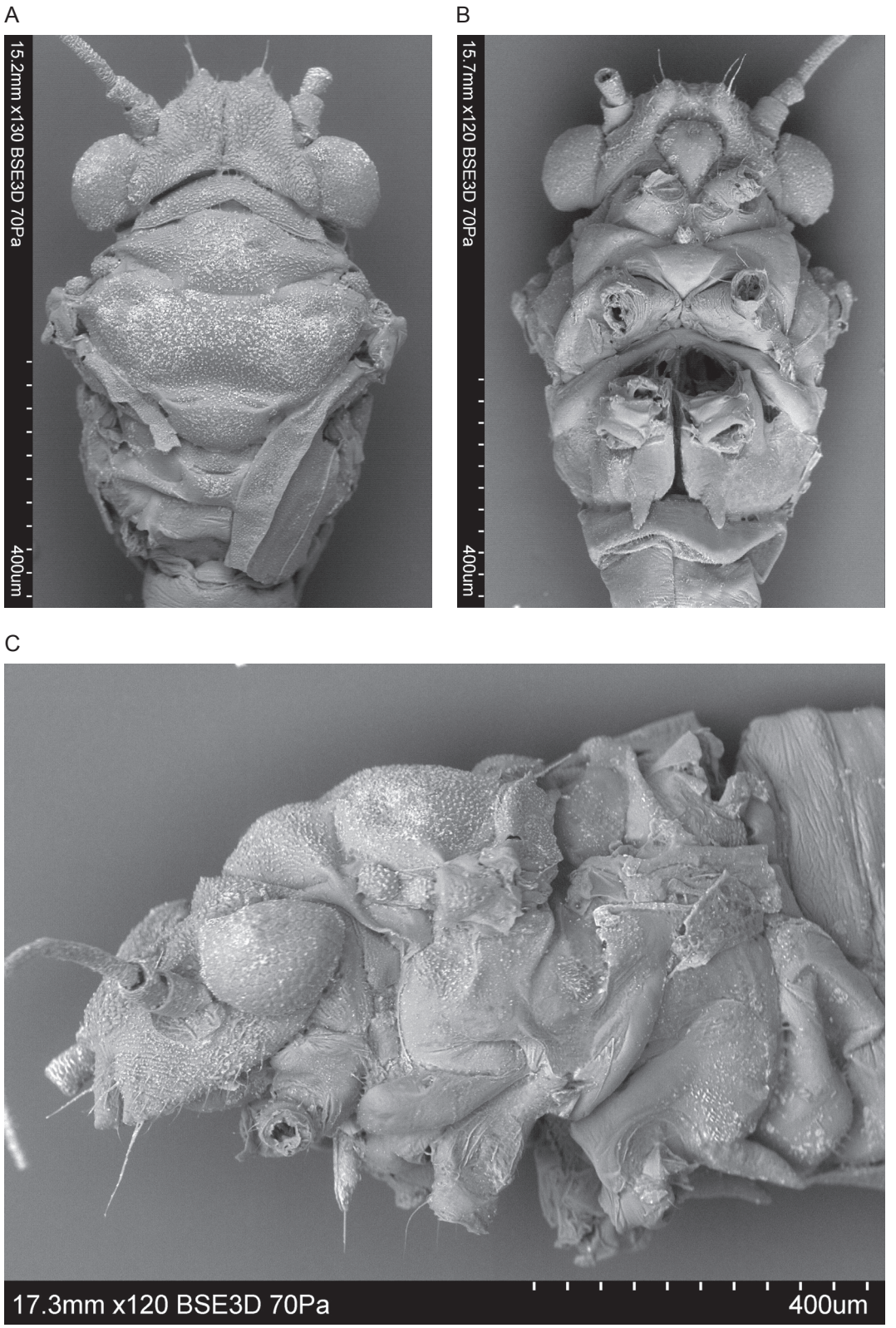


Fig. 42. *Russelliana solanicola* Tuthill, 1959; **A** – dorsal side, **B** – ventral side, **C** – lateral side

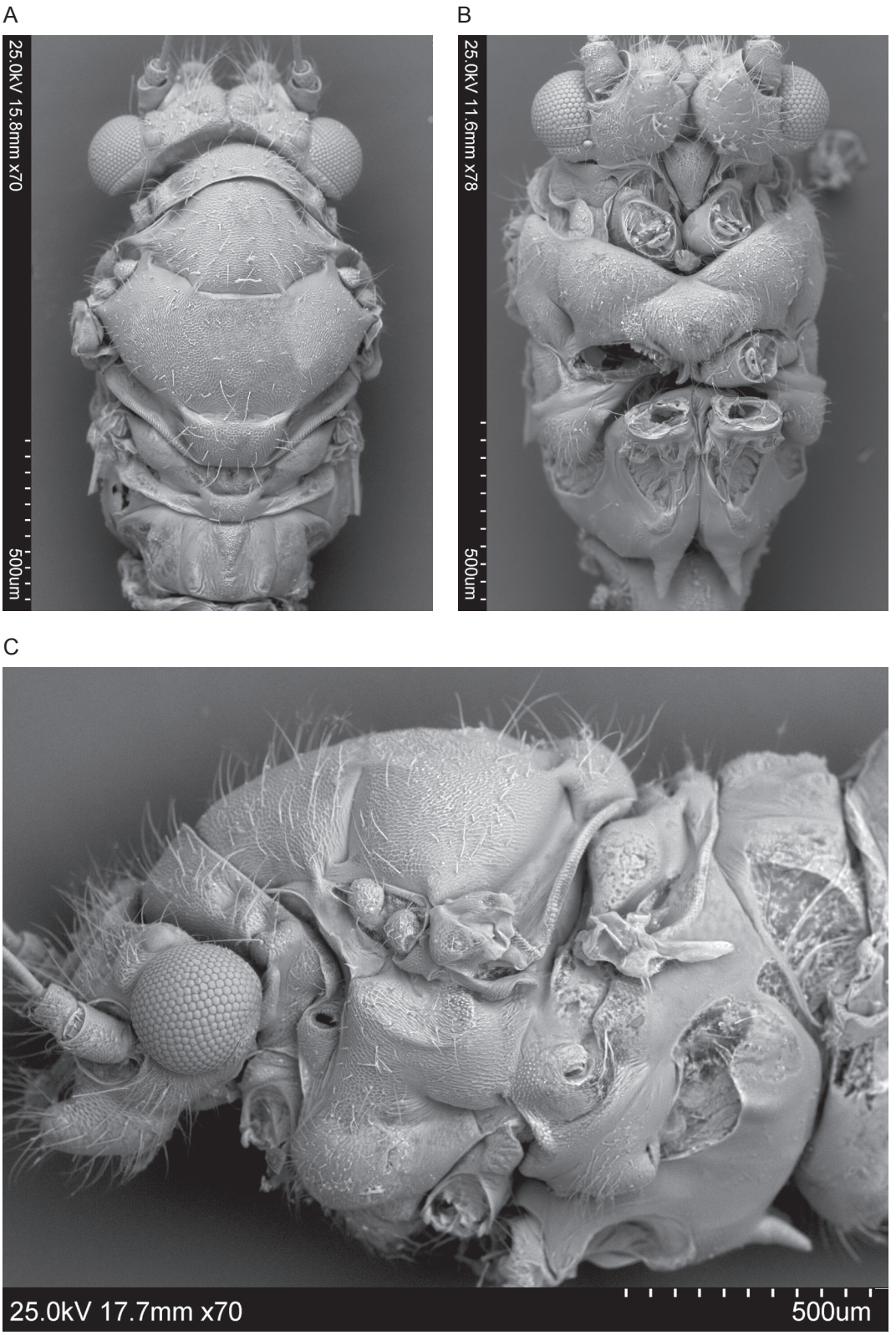


Fig. 43. *Auchmerina tuthilli* Klimaszewski, 1962; **A** – dorsal side, **B** – ventral side, **C** – lateral side

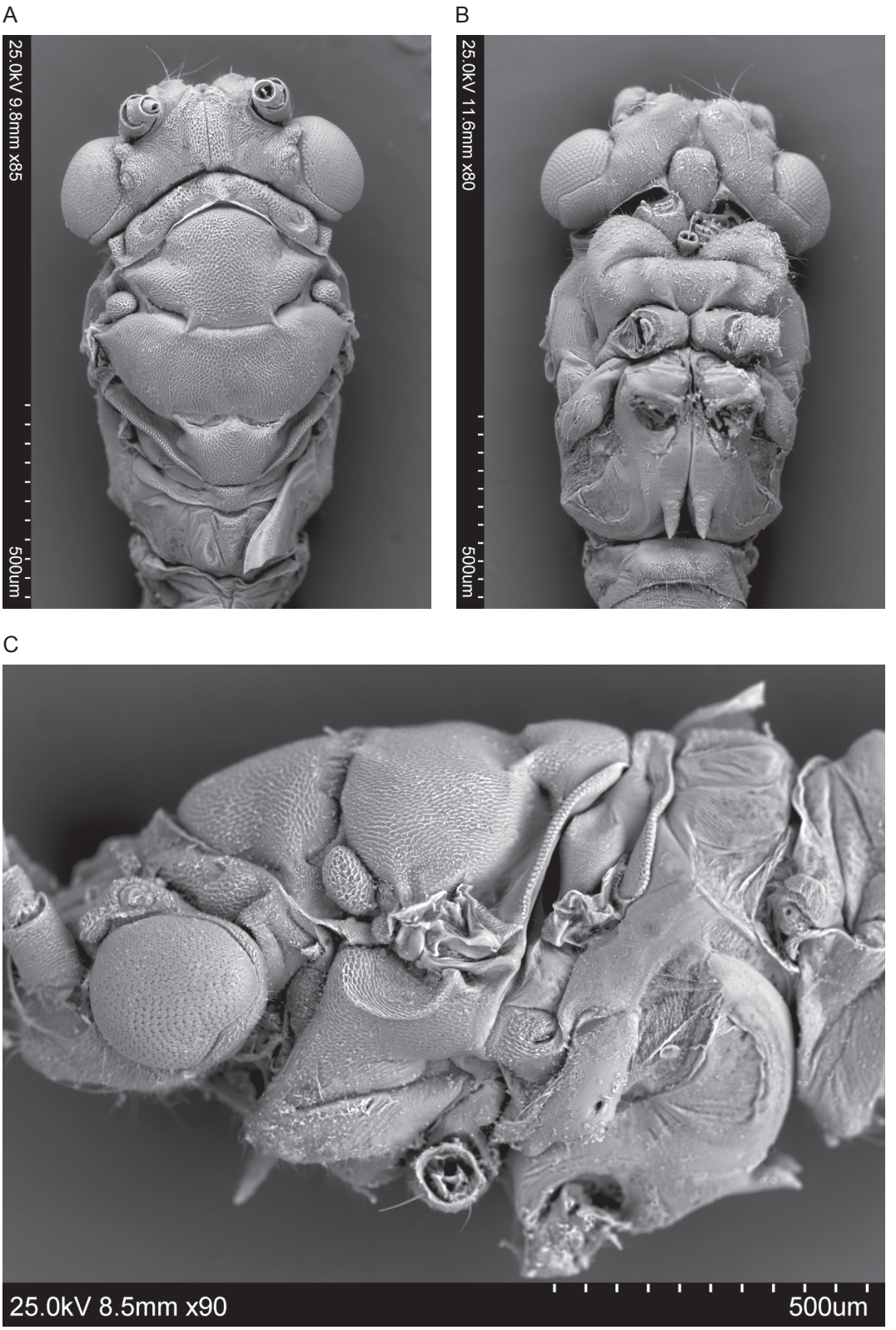


Fig. 44. *Ciriacremum nigripes* Hollis, 1976; **A** – dorsal side, **B** – ventral side, **C** – lateral side

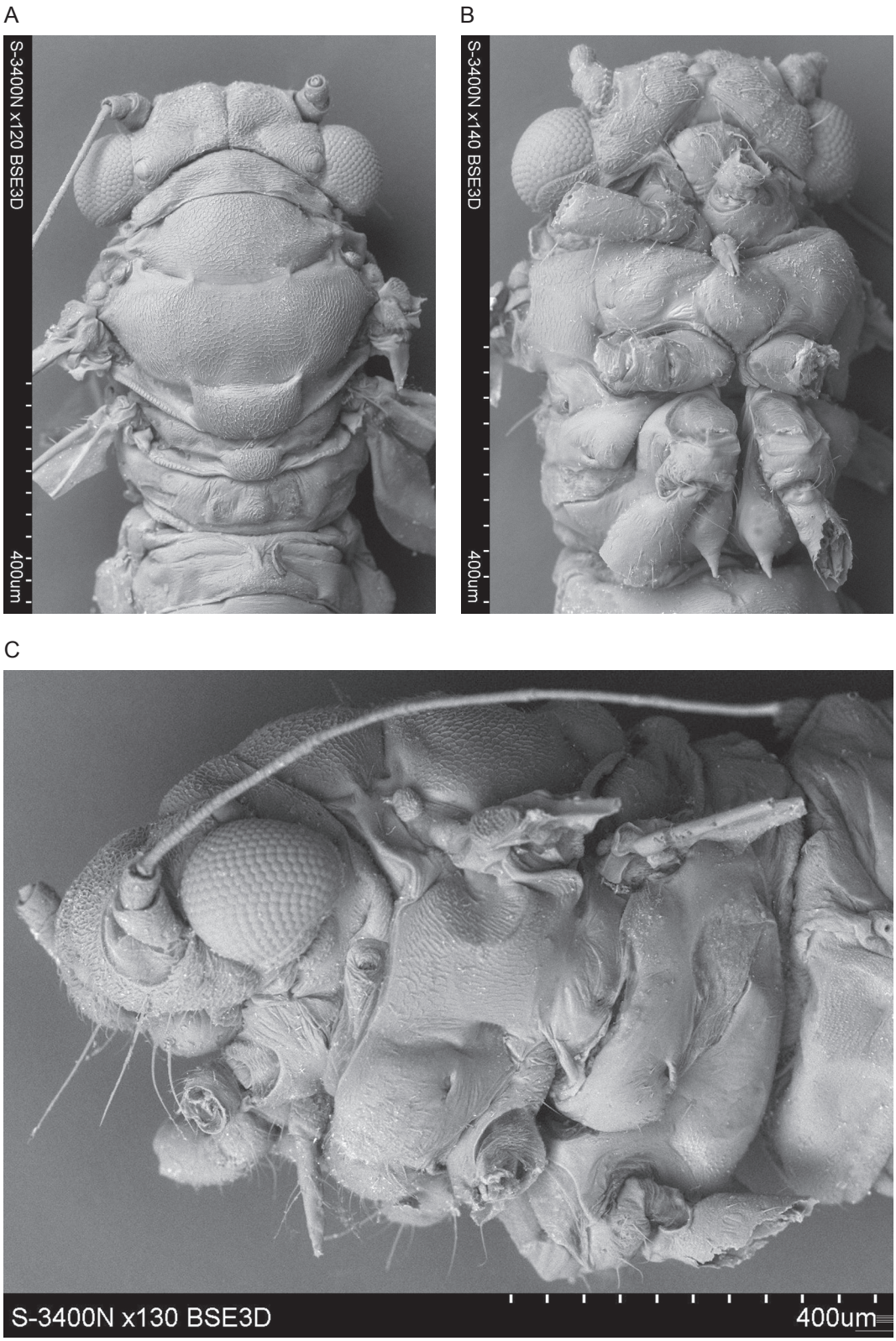


Fig. 45. *Heteropsylla cubana* Crawford, 1914; **A** – dorsal side, **B** – ventral side, **C** – lateral side

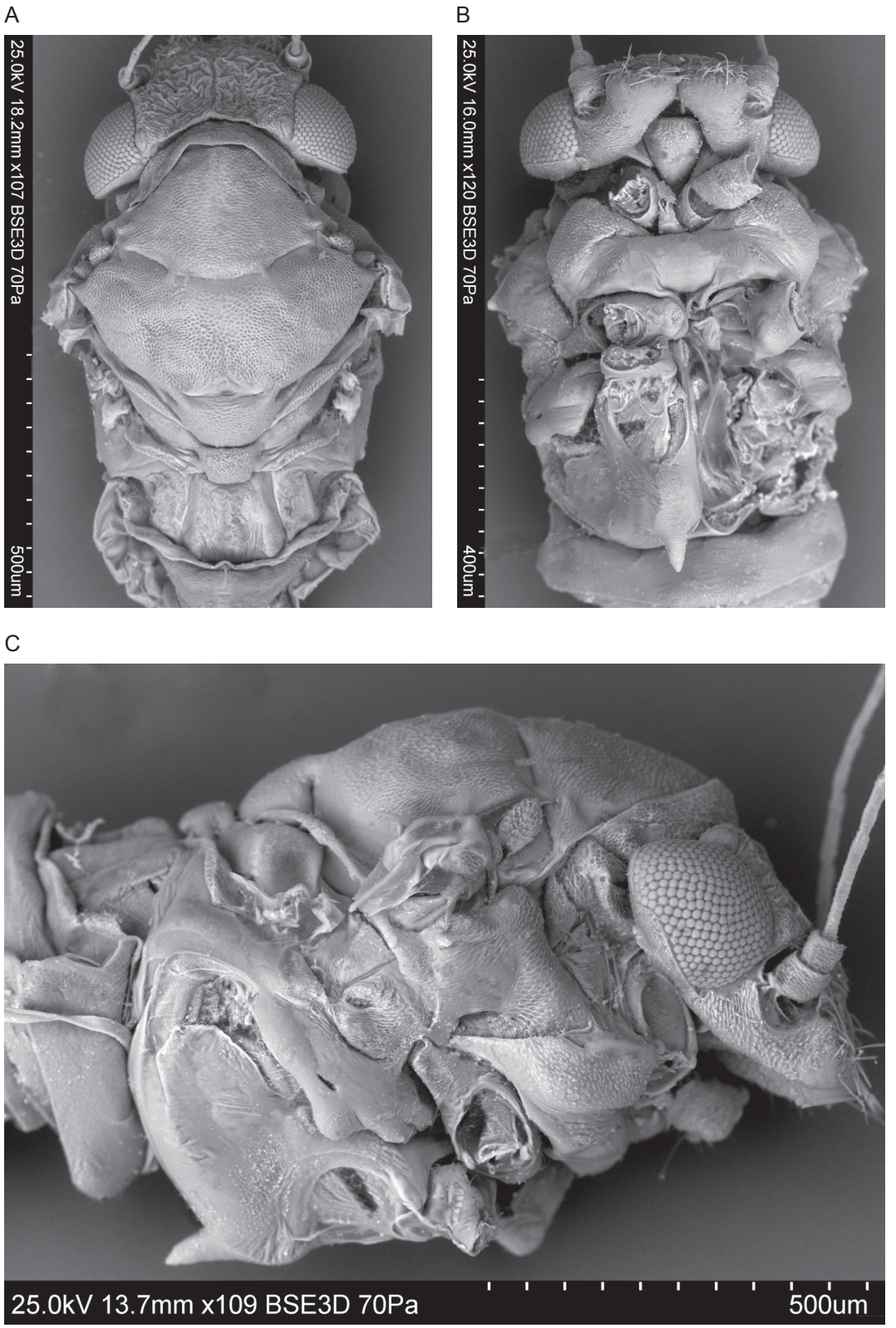


Fig. 46. *Euphalerus vittatus* Crawford, 1912; **A** – dorsal side, **B** – ventral side, **C** – lateral side

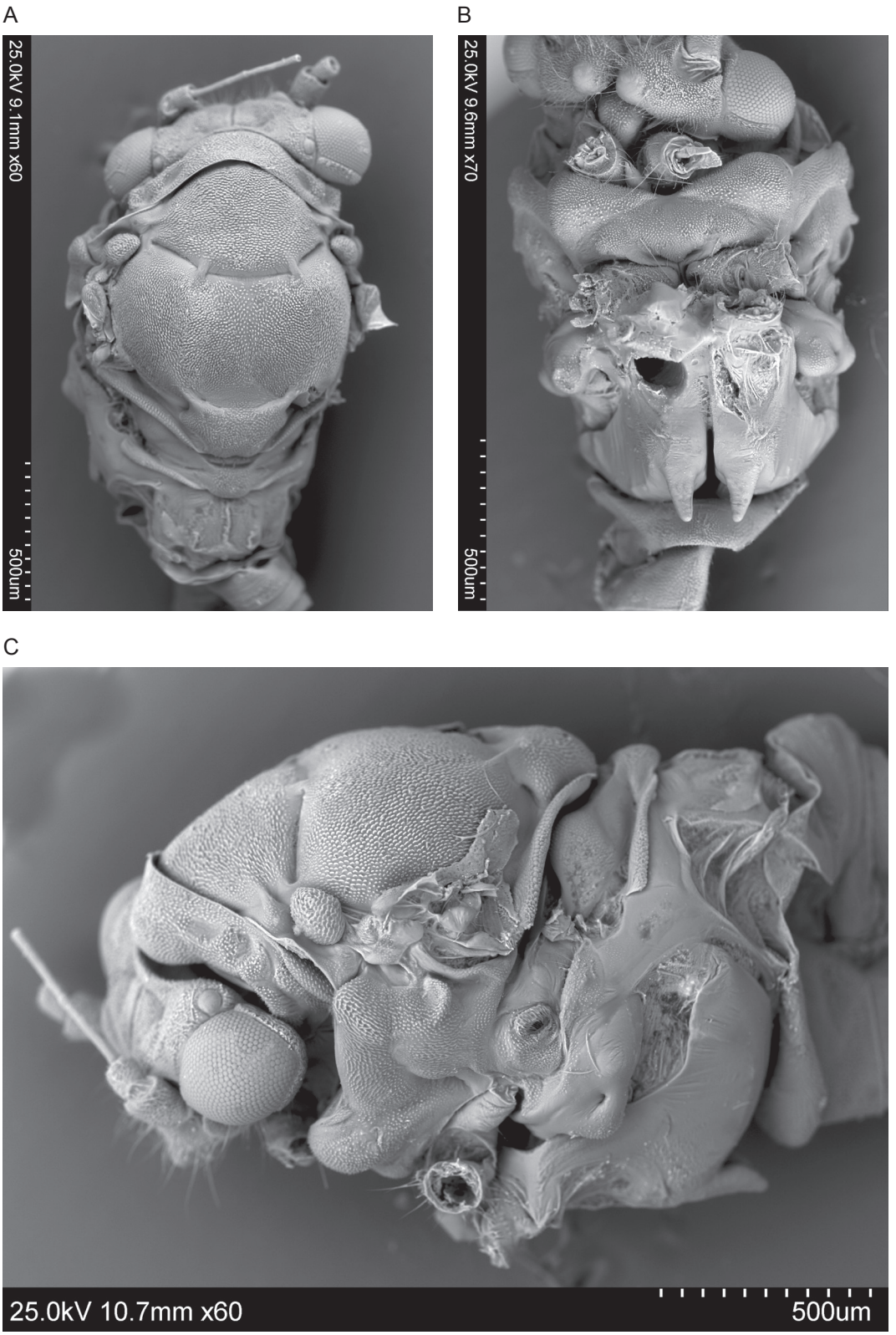


Fig. 47. *Anomoneura mori* Schwarz, 1896; **A** – dorsal side, **B** – ventral side, **C** – lateral side

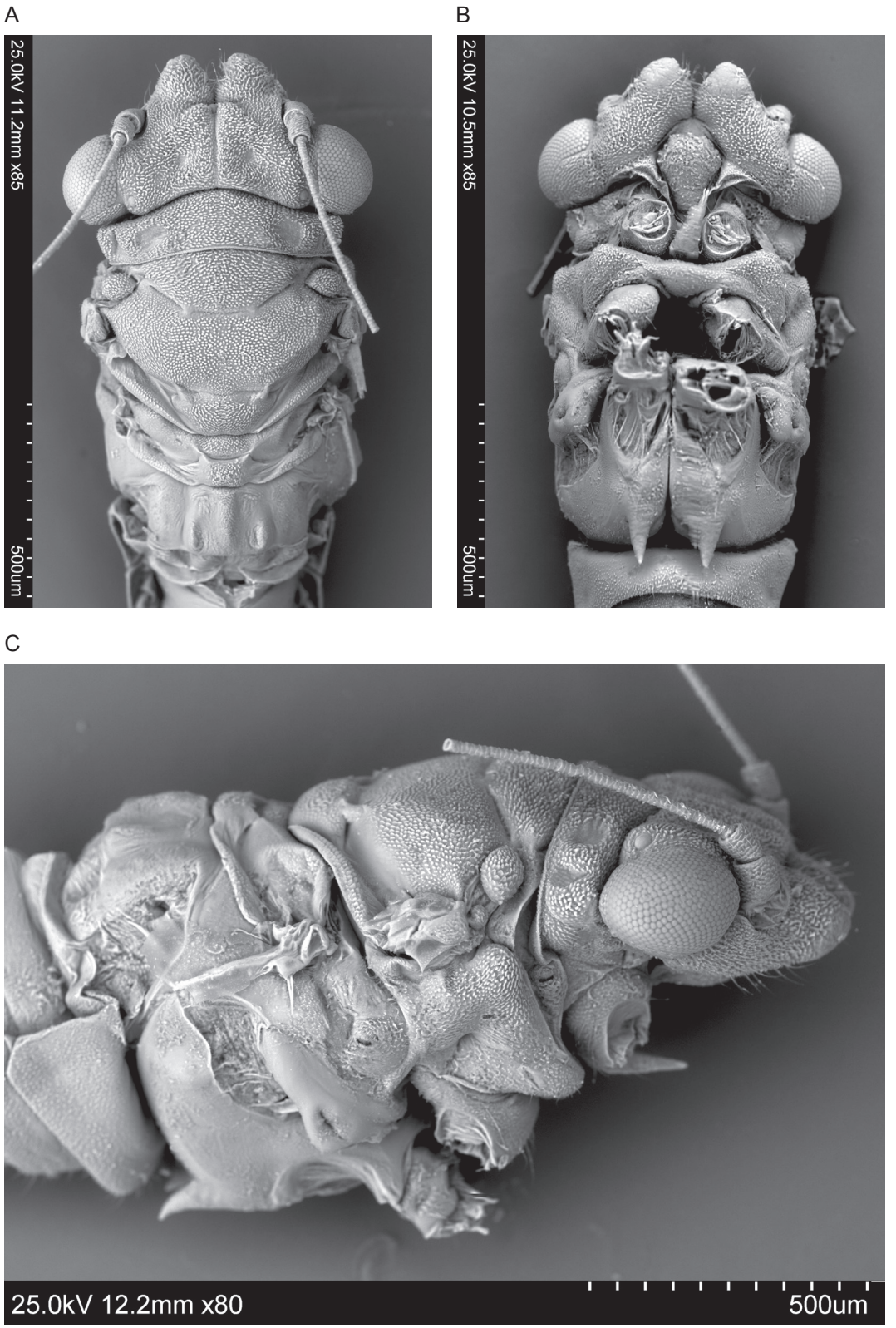


Fig. 48. *Arytaina maculata* (Löw, 1886); **A** – dorsal side, **B** – ventral side, **C** – lateral side

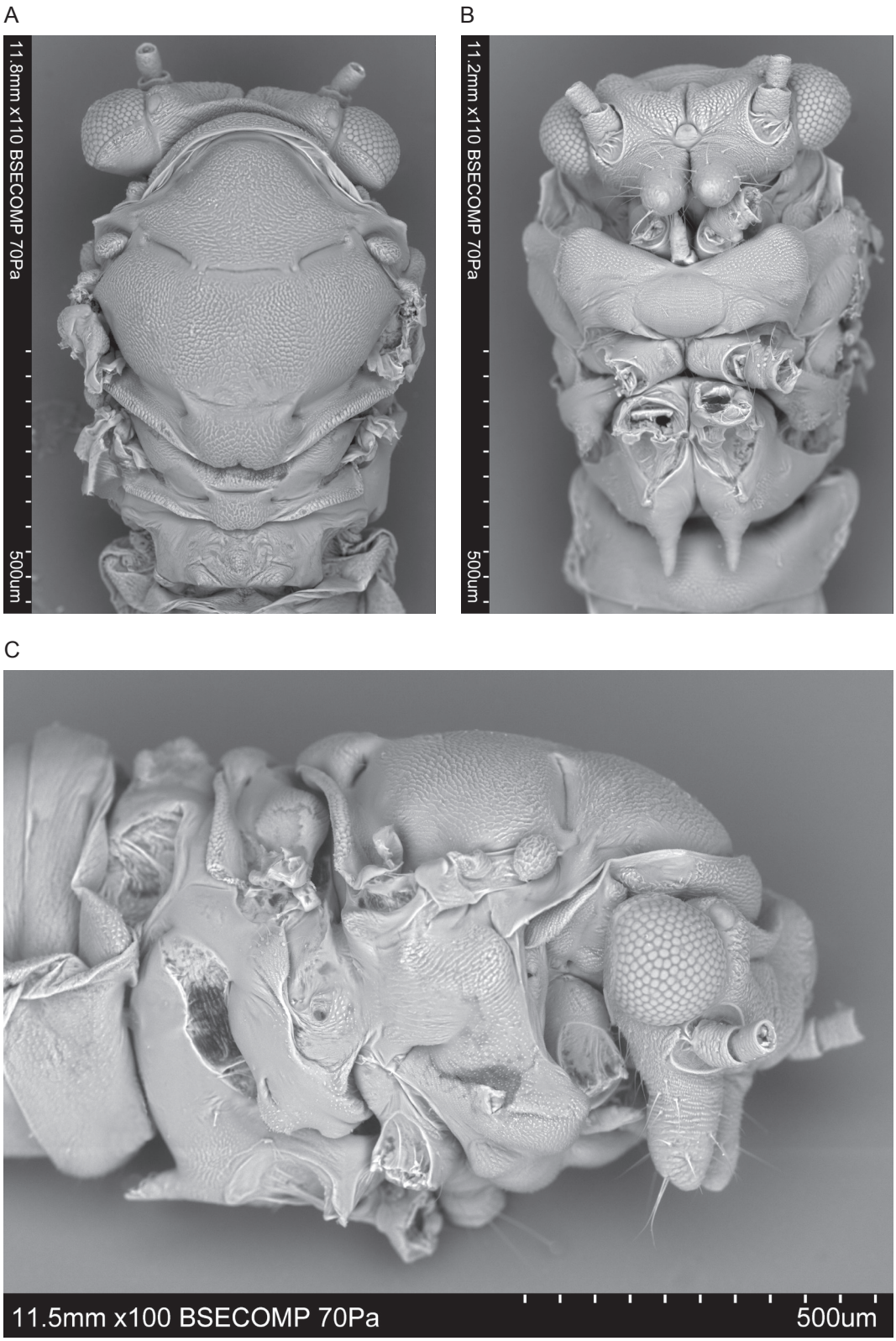


Fig. 49. *Cacopsylla ambiqua* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side (after Drohojowska et al. 2013)

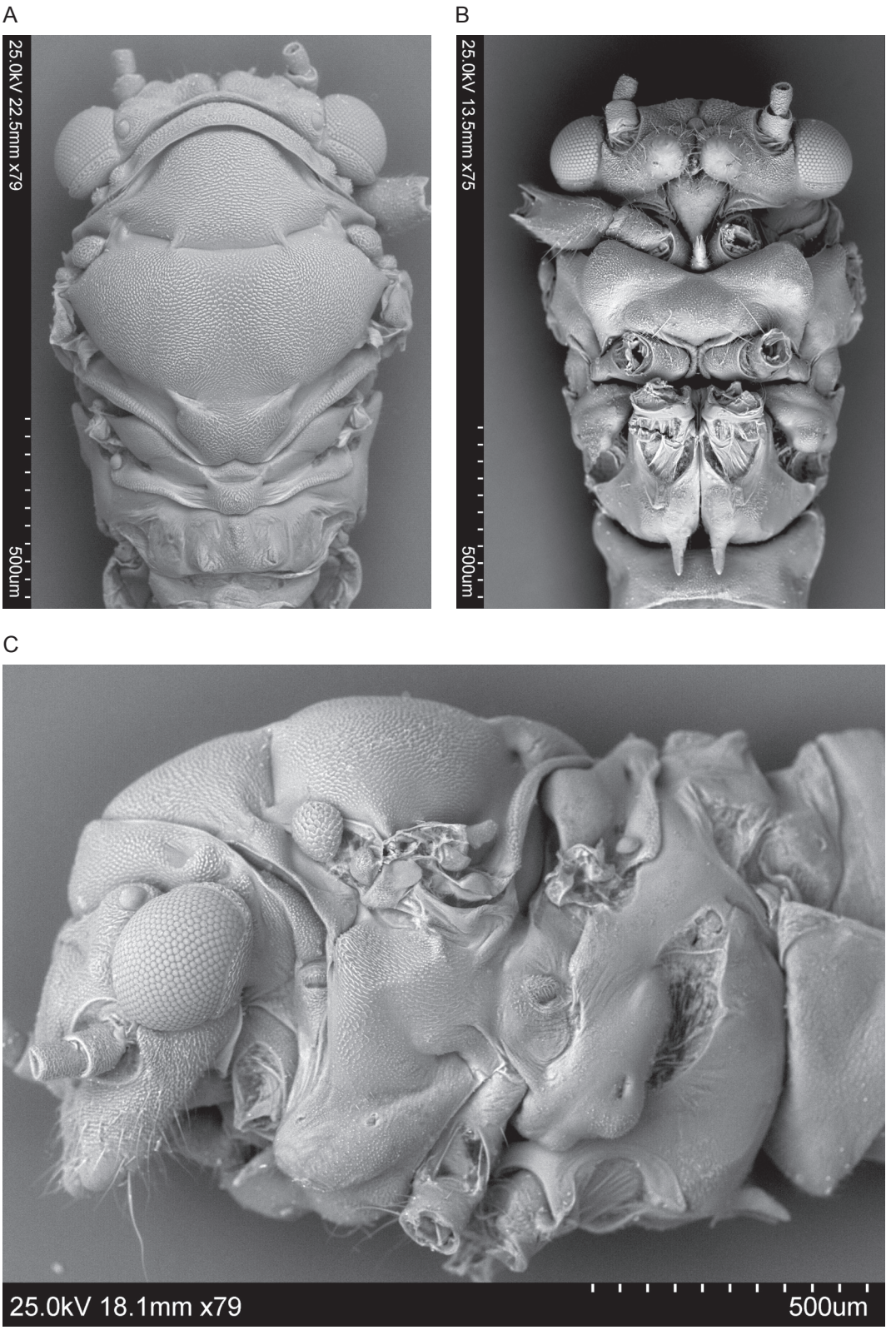


Fig. 50. *Cacopsylla crataegi* (Schrank, 1801); **A** – dorsal side, **B** – ventral side, **C** – lateral side (after Drohojowska et al. 2013)

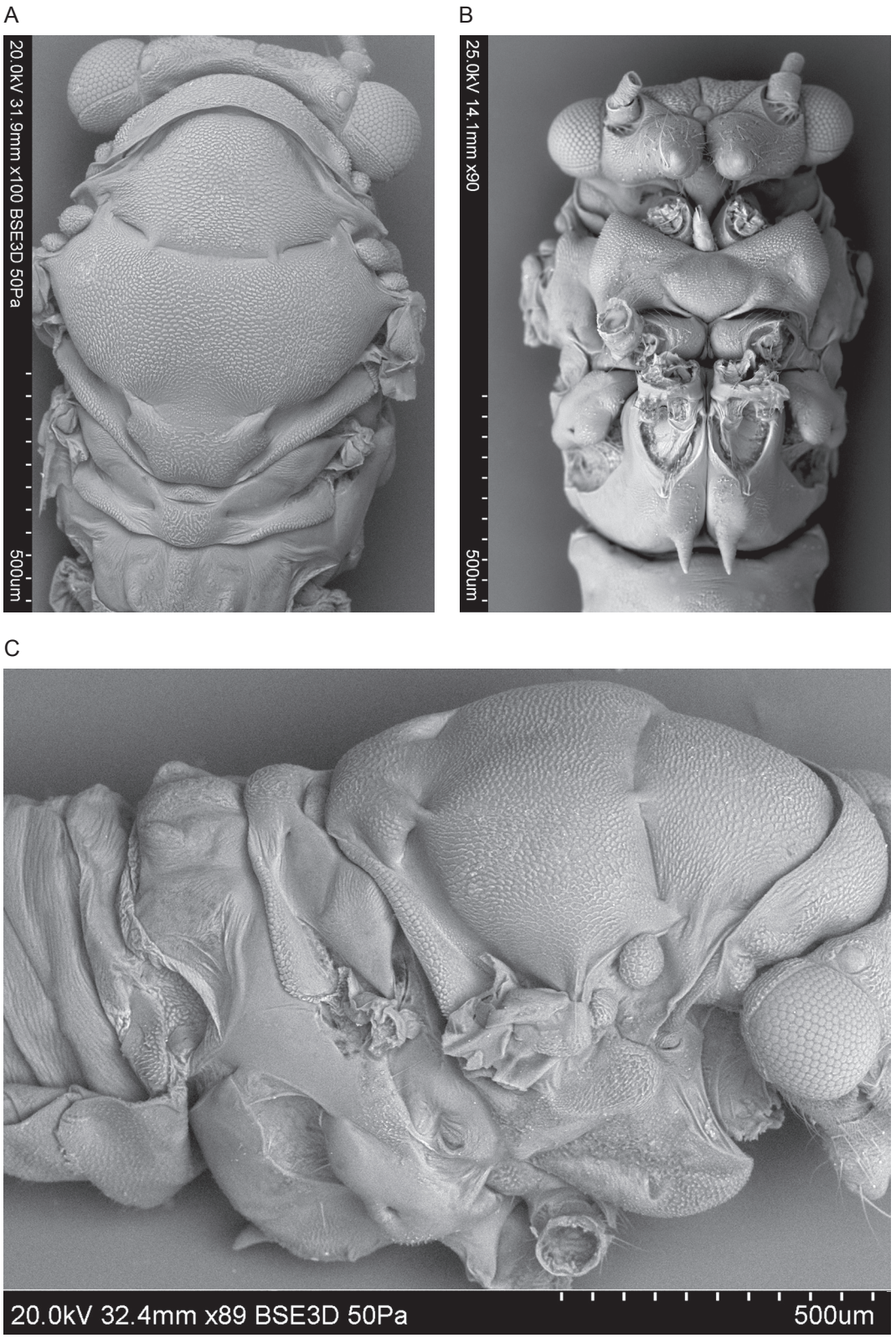


Fig. 51. *Cacopsylla peregrina* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side (after Drohojowska et al. 2013)

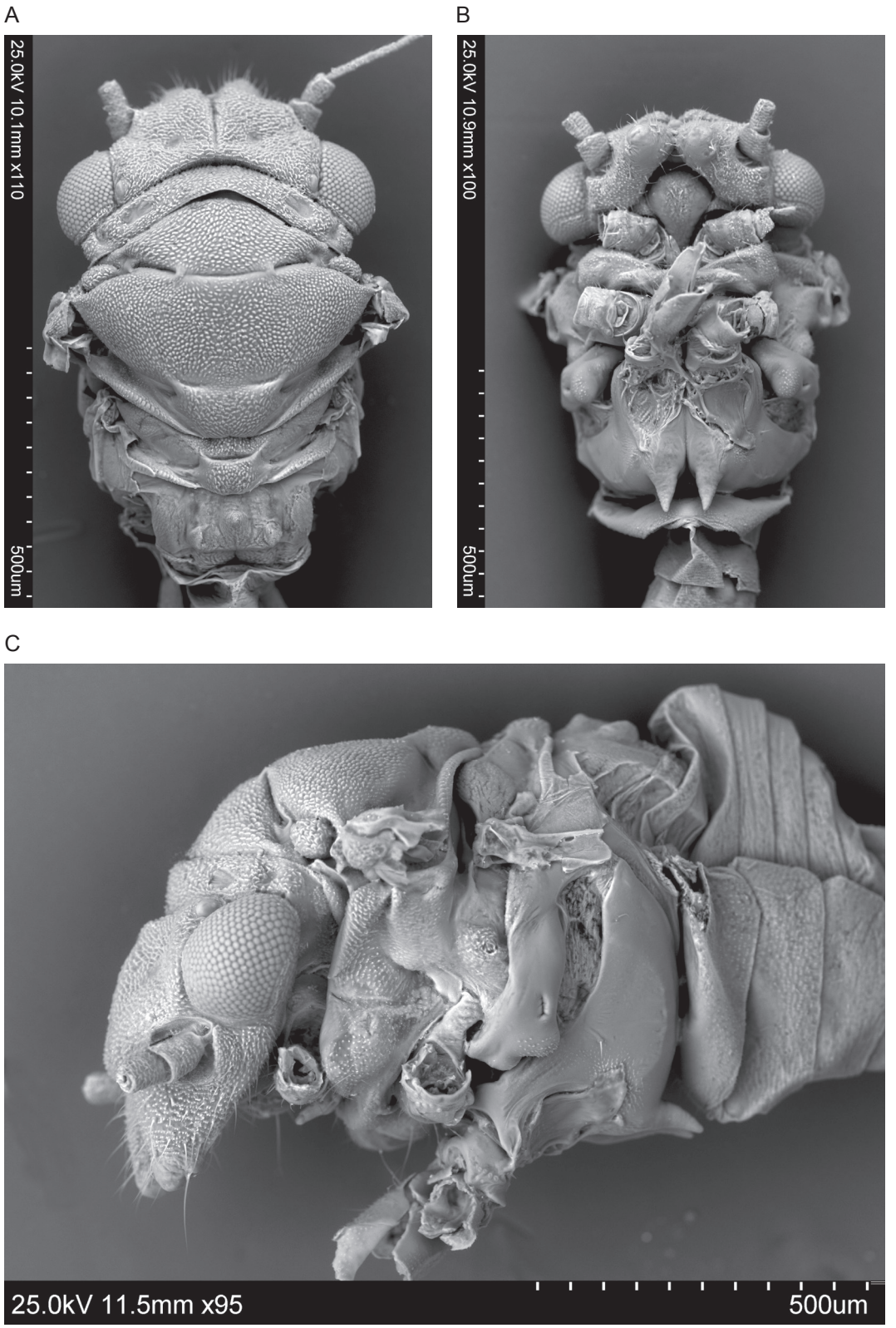


Fig. 52. *Cyamophila bajevae* Loginova, 1978; **A** – dorsal side, **B** – ventral side, **C** – lateral side

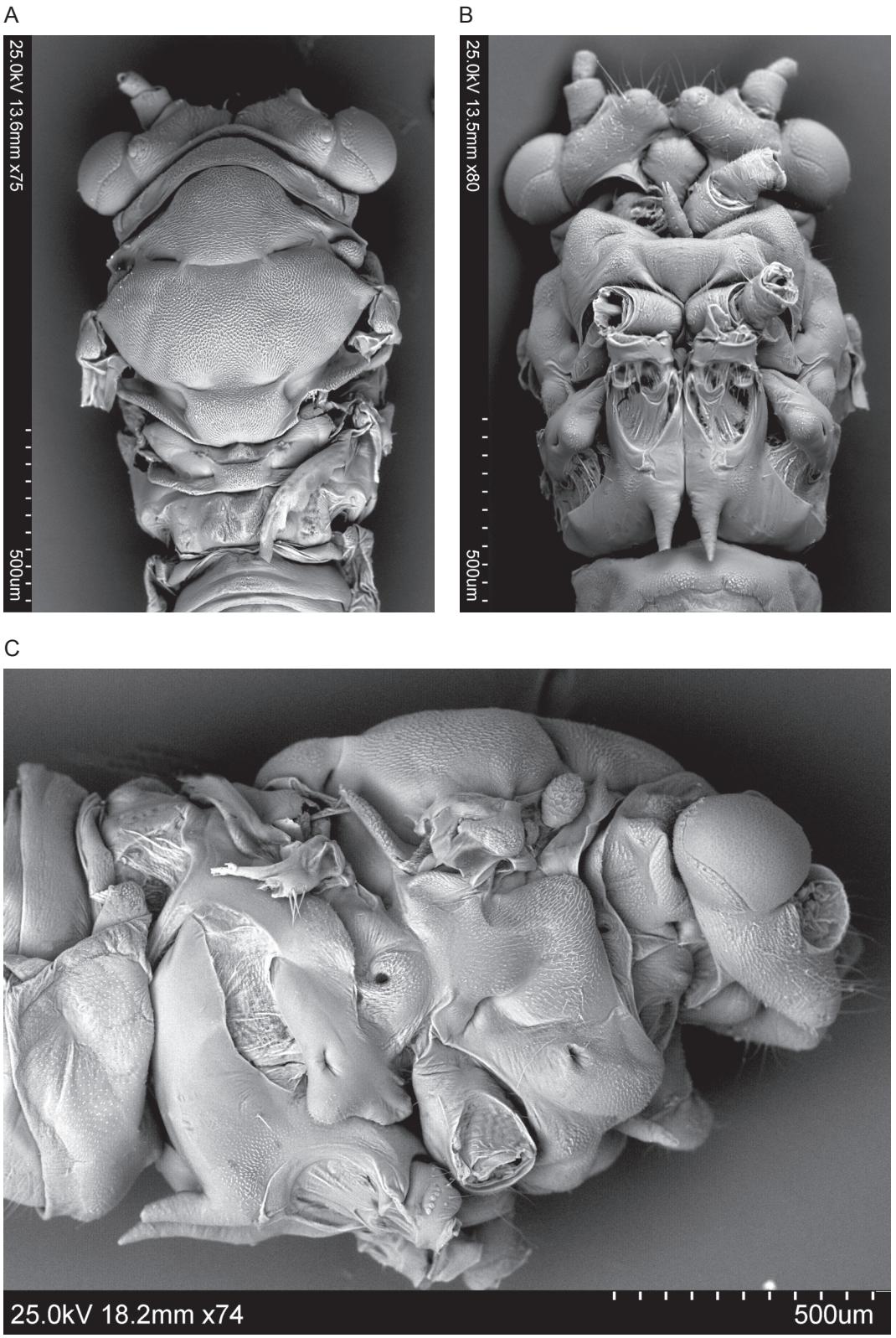


Fig. 53. *Psylla foersteri* Flor, 1861; **A** – dorsal side, **B** – ventral side, **C** – lateral side

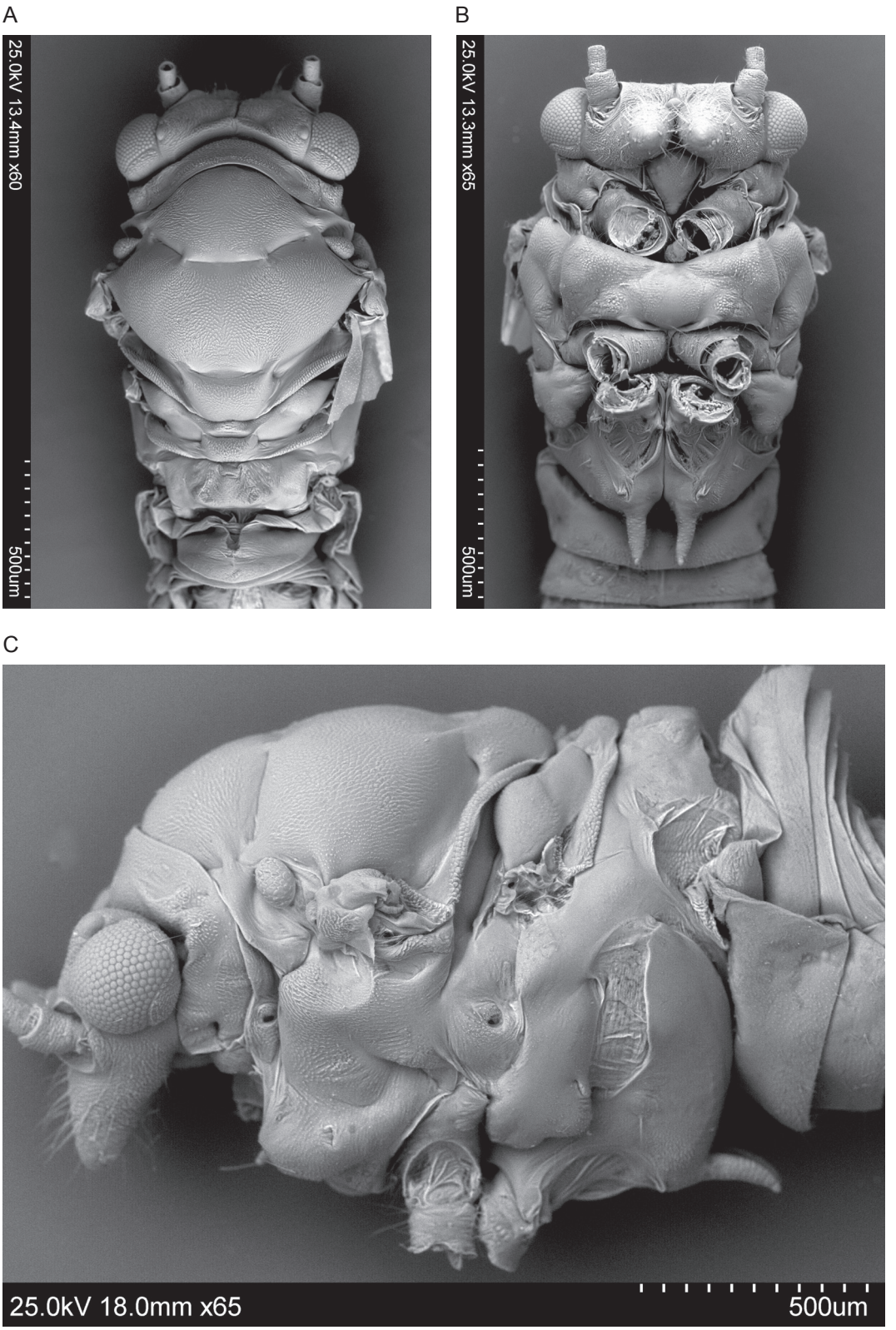


Fig. 54. *Psylla fusca* Zetterstedt, 1828; **A** – dorsal side, **B** – ventral side, **C** – lateral side

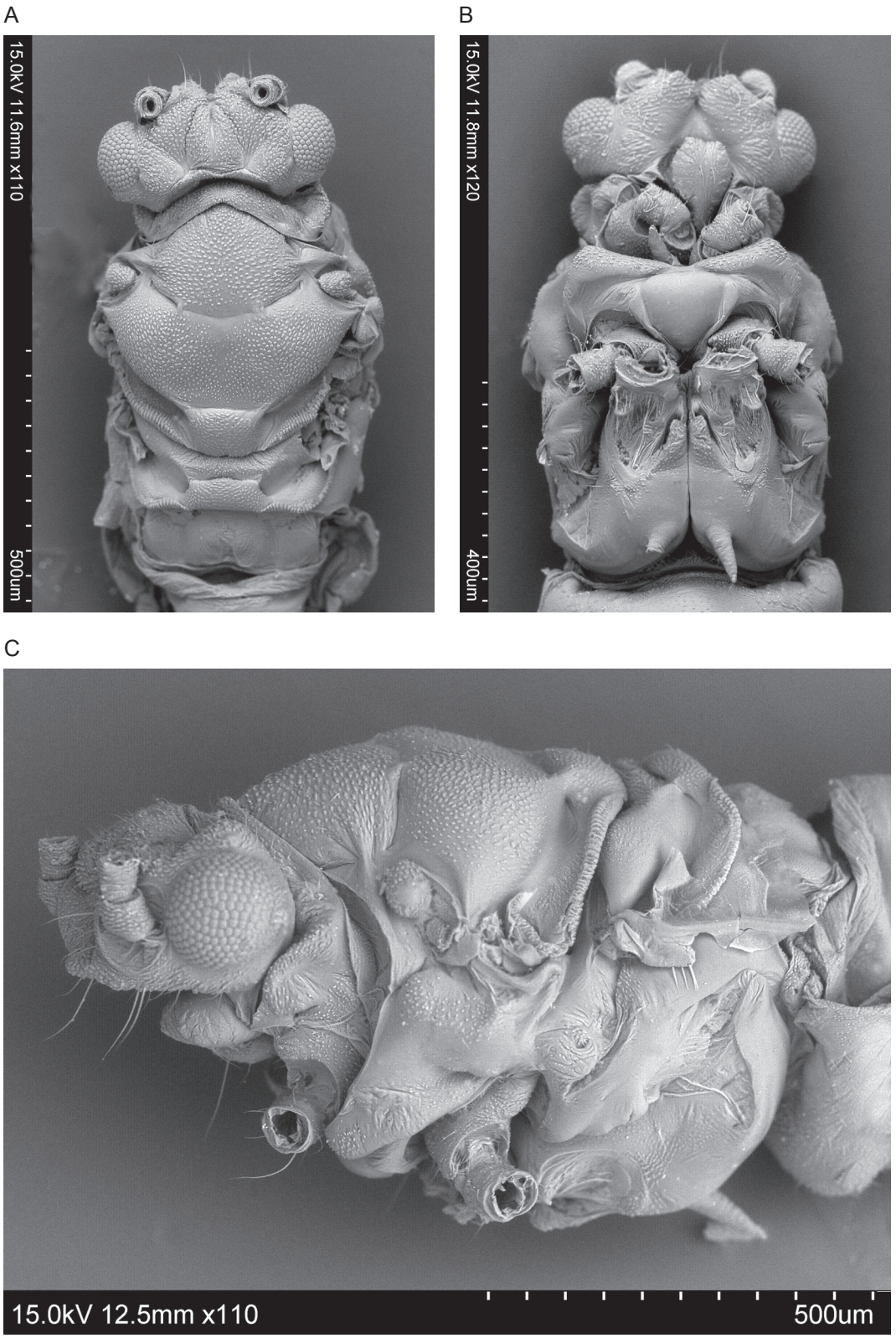


Fig. 55. *Bactericera bielawskii* (Klimaszewski, 1963); **A** – dorsal side, **B** – ventral side, **C** – lateral side

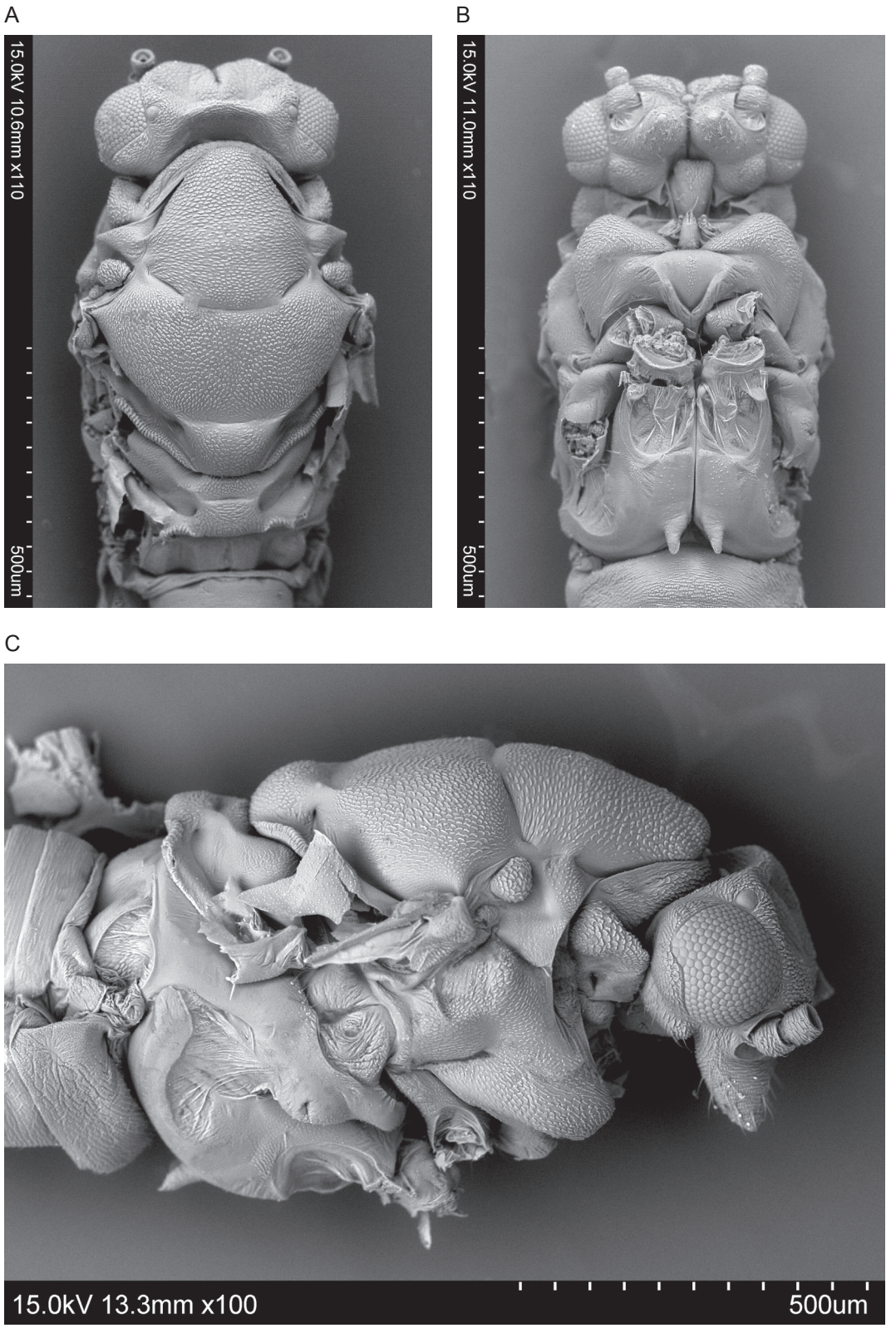


Fig. 56. *Bactericera curvatinervis* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side

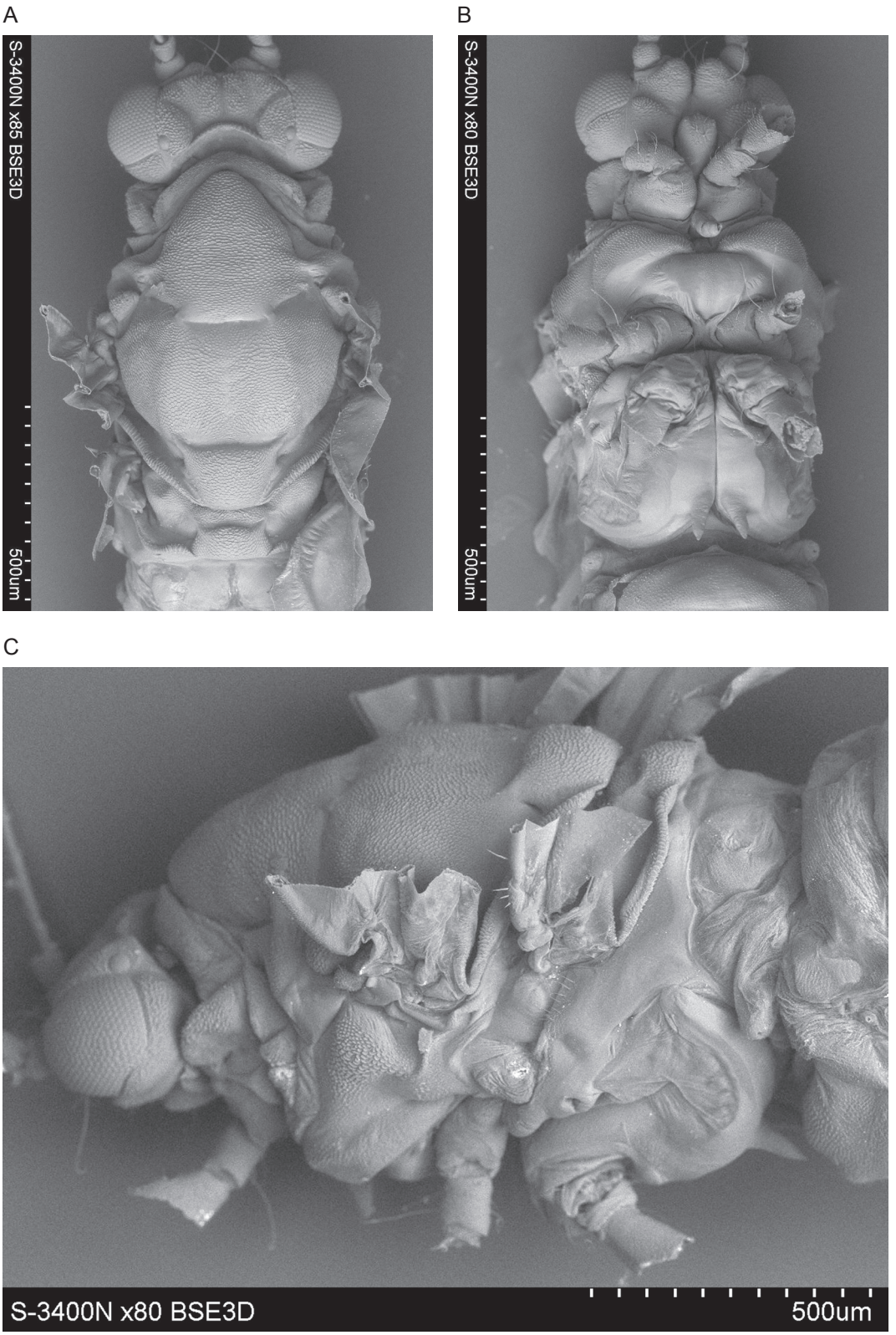


Fig. 57. *Calinda pehuenche* (Olivares and Burckhardt, 1997); **A** – dorsal side, **B** – ventral side, **C** – lateral side

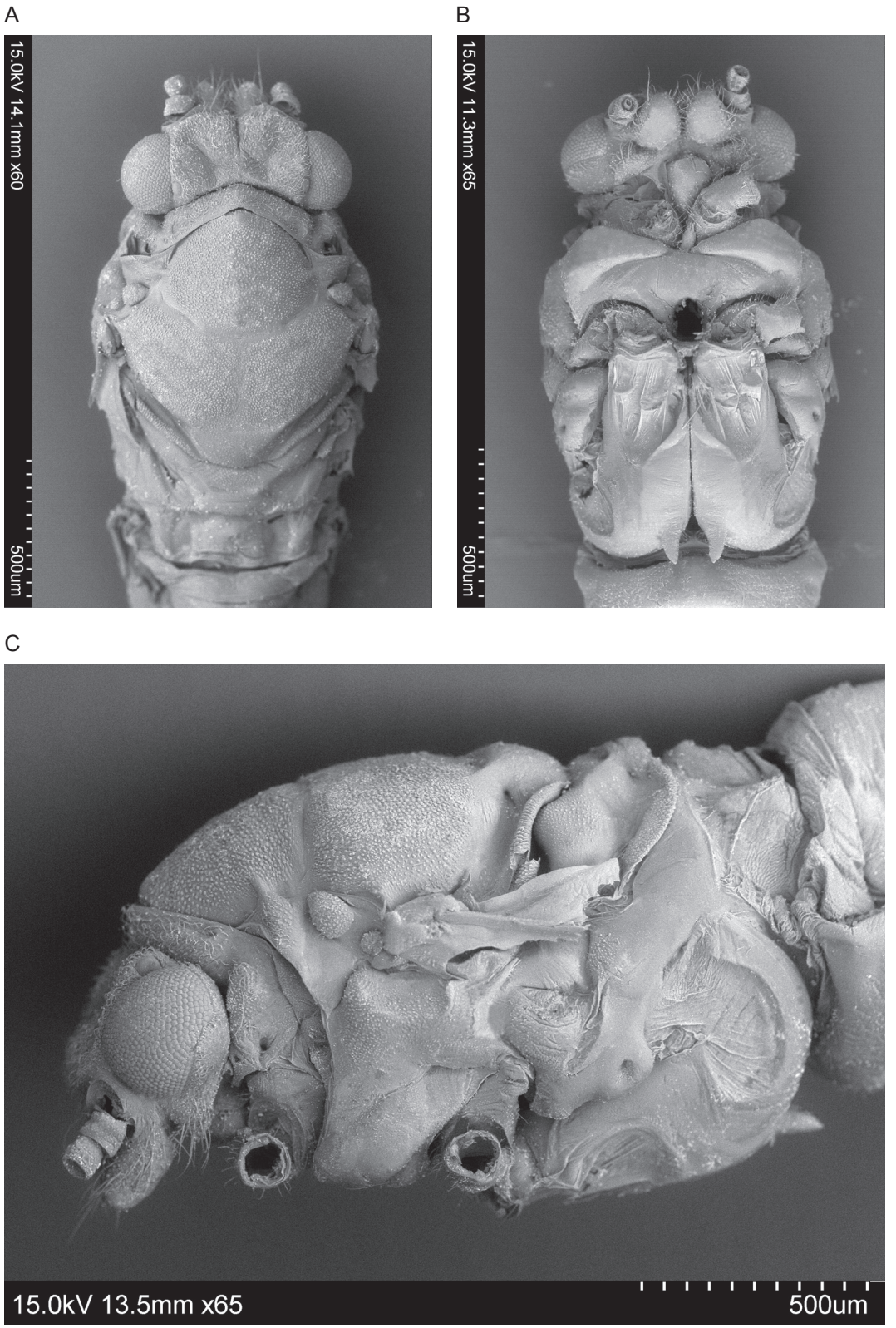


Fig. 58. *Egeirotrioza ceardi* (Bergevin, 1926); **A** – dorsal side, **B** – ventral side, **C** – lateral side

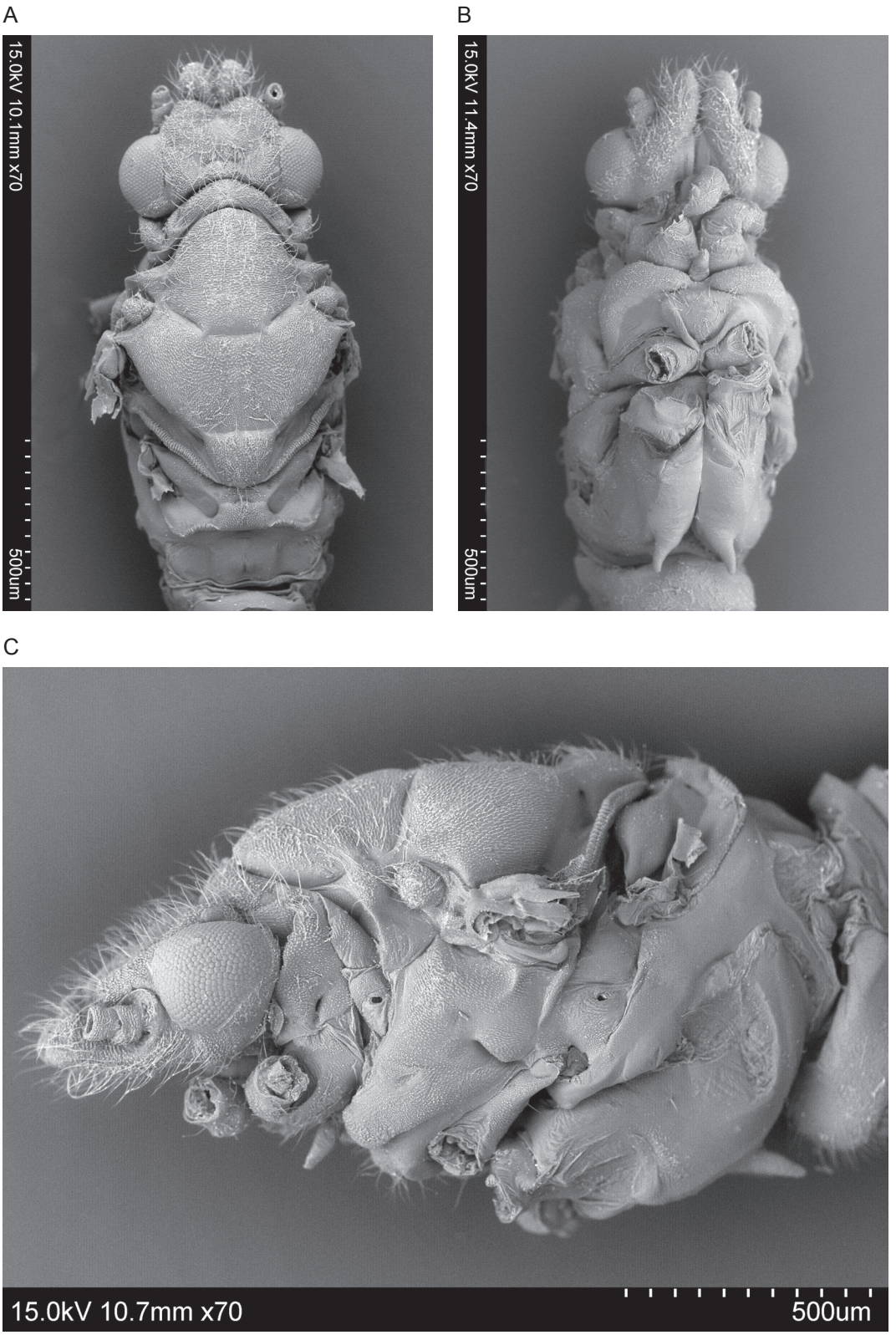


Fig. 59. *Trichochermes walkeri* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side

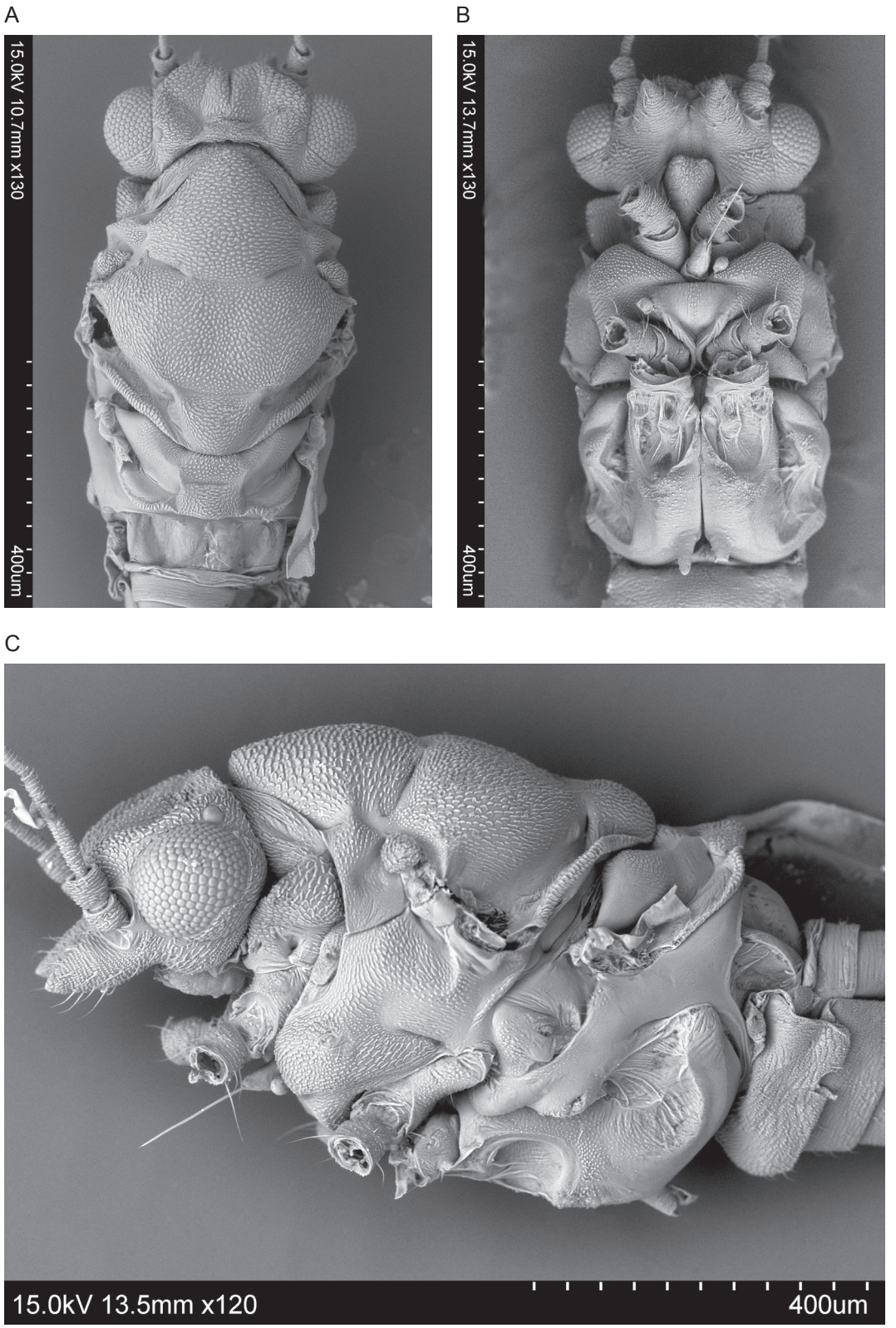


Fig. 60. *Trioza anthrisci* (Burckhardt, 1986); **A** – dorsal side, **B** – ventral side, **C** – lateral side

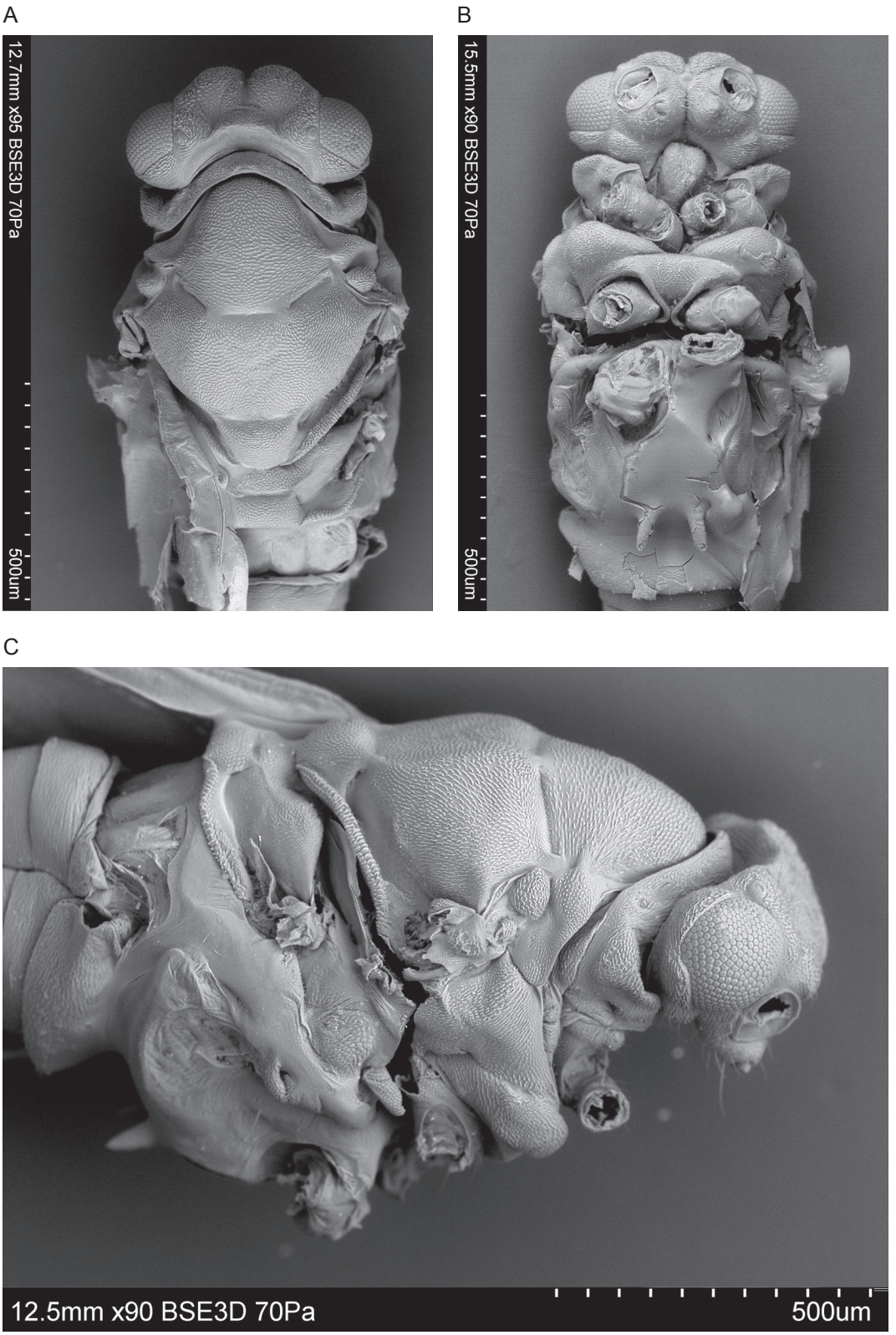


Fig. 61. *Trioza berberidis* (Burckhardt, 1988); **A** – dorsal side, **B** – ventral side, **C** – lateral side

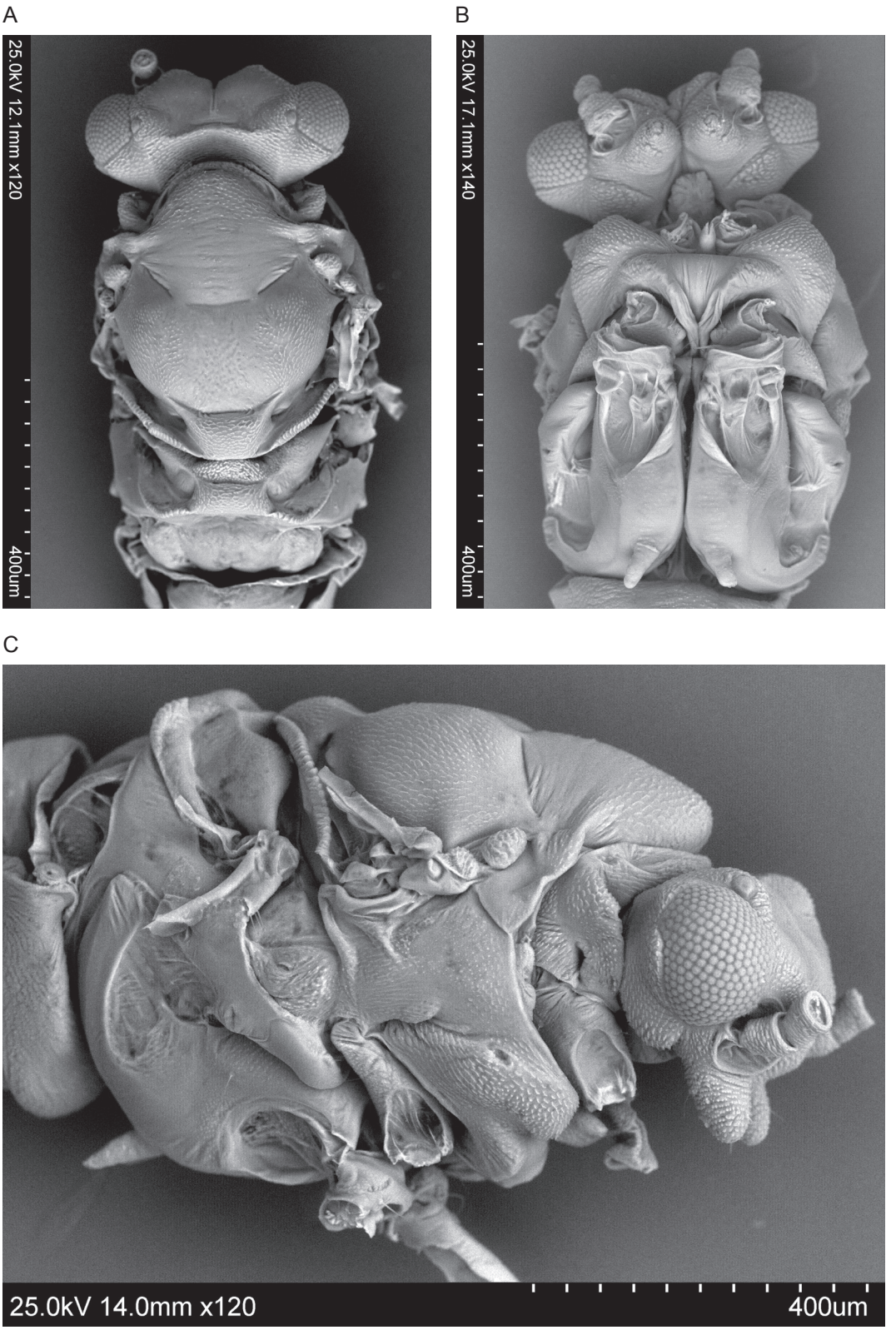


Fig. 62. *Trioza galii* (Foerster, 1848); **A** – dorsal side, **B** – ventral side, **C** – lateral side

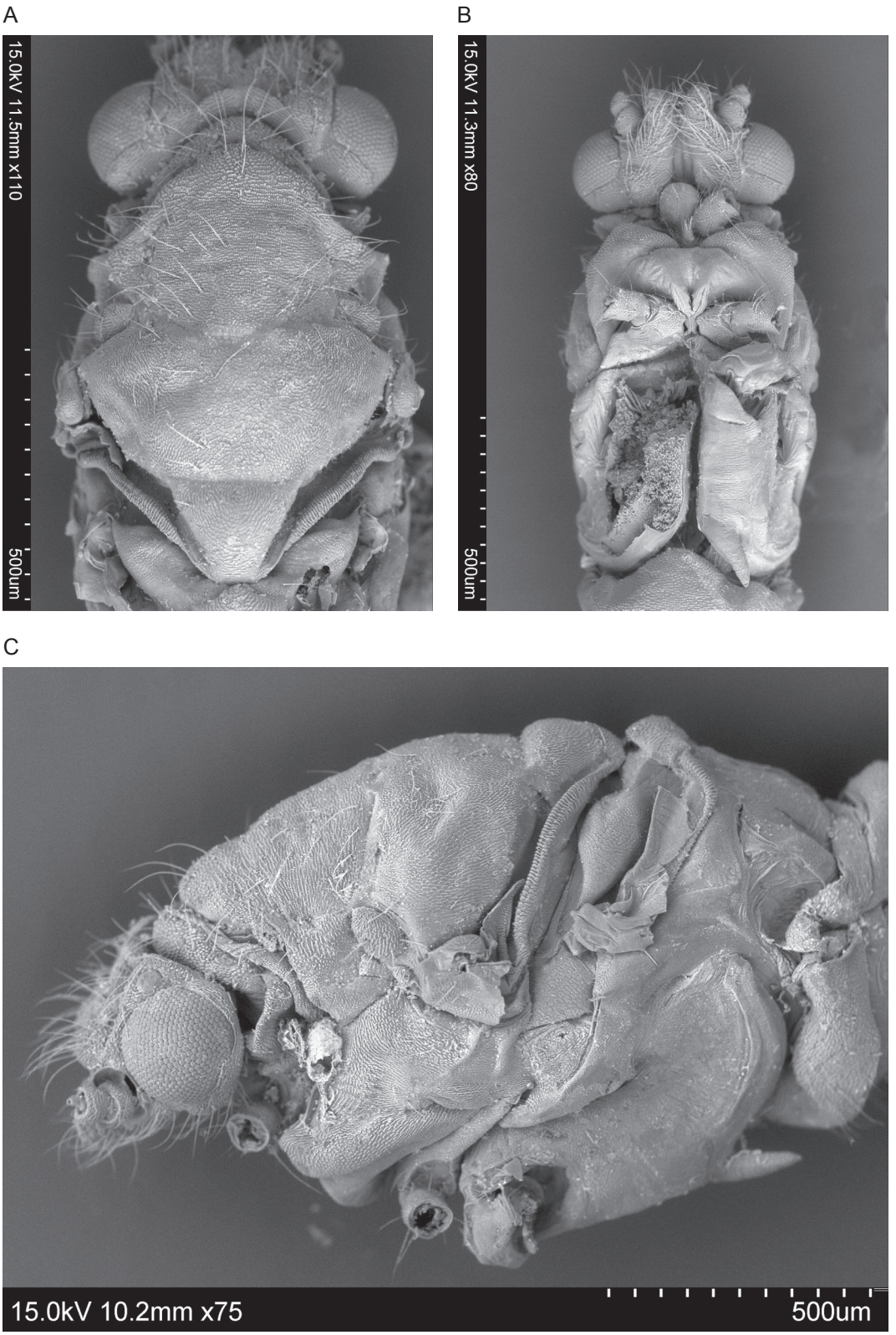


Fig. 63. *Trioza malloticola* (Crawford, 1928); **A** – dorsal side, **B** – ventral side, **C** – lateral side

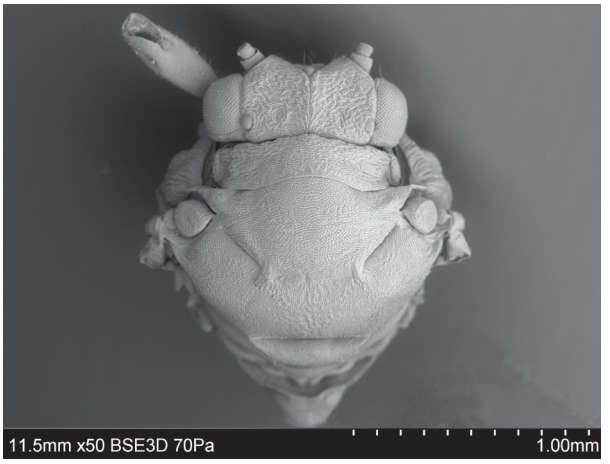


Fig. 64. *Caillardia robusta* (Loginova, 1956); part of dorsal side

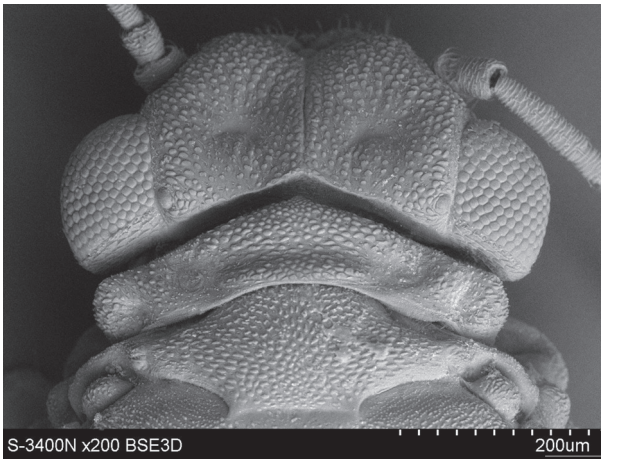


Fig. 65. *Blastopsylla occidentalis* (Taylor, 1985); part of dorsal side

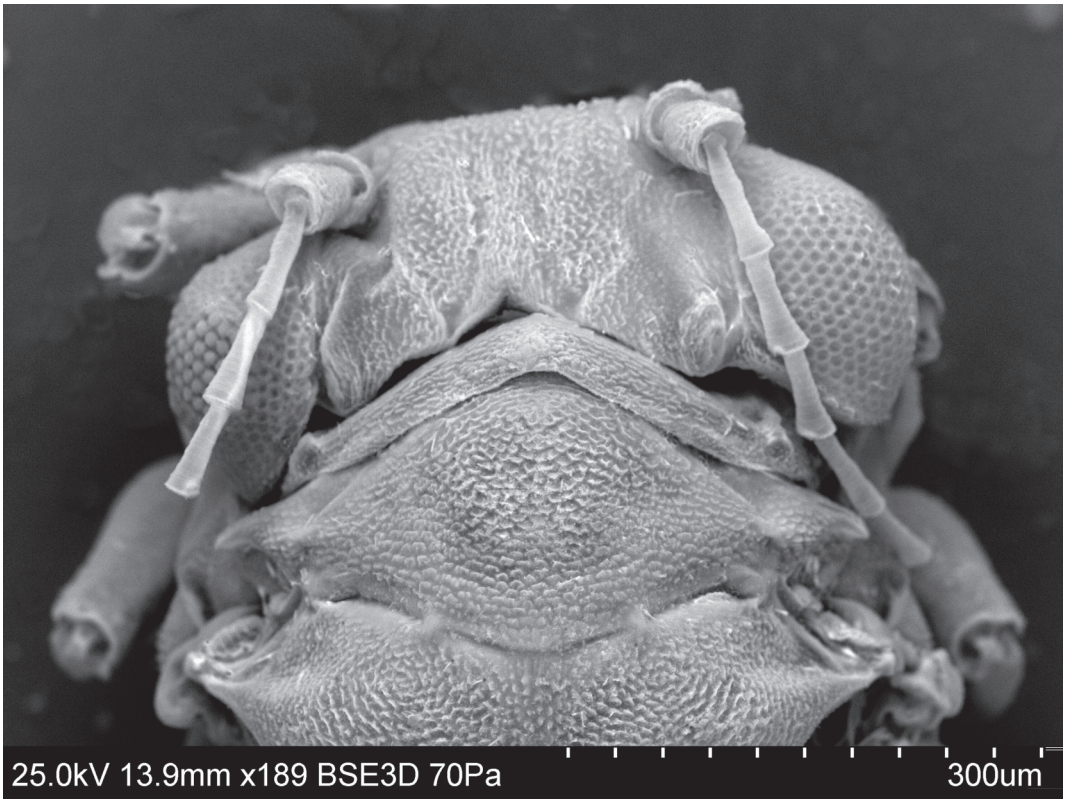


Fig. 66. *Pseudophacopteron zimmermanni* (Aulmann, 1912); part of dorsal side

2.2. Palaeontological data

Psyllids or jumping plant-lice is a group present in the fossil record since the early Jurassic (Klimaszewski 1997a, Grimaldi, Engel 2005). Becker-Migdisova (1985) provided a classification of psyllids representing three Mesozoic families: Liadopsyllidae Martynow 1927, Malmopsyllidae and Neopsylloididae. After an analysis of the wings, Klimaszewski and Wojciechowski (1992) made the Neopsylloididae Becker-Migdisova, 1985 and Malmopsyllidae Becker-Migdisova, 1985 families synonymous. The species of the Malmopsyllidae family have gone extinct in the Early Cretaceous (Klimaszewski 1997a). The youngest species – *Liadopsylla hesperia* Ouvrard and Burckhardt, 2010, classified in another, also extinct family Liadopsyllidea, lived in the Late Cretaceous (Turonian, approximately 90 million years ago) (Ouvrard et al. 2010). In the fossil material representing the subsequent 46 million years (from Late Cretaceous through Paleocene), no occurrence of psyllids has been confirmed, until the Middle Eocene (44 million years ago). The representatives of insects of the *Eogyropsylla* Klimaszewski 1997, described from inclusions in Baltic amber (Klimaszewski 1997c, Drohojowska 2011, Ouvrard et al. 2013) and from the imprints from the Kishenehn Formation, Montana, USA (Ouvrard et al. 2013) occurred in that period. The cause of the lack of data regarding psyllids in the fossil material is still unknown, but it is presumed that it might be related to changes in the flora of the Mid-Cretaceous (Klimaszewski 1997a, Ouvrard et al. 2010). *Eogyropsylla paveloctogenarius* Ouvrard Burckhardt and Greenwalt, 2013 is the oldest Eocene species representing the extant family of Aphalaridae (Ouvrard et al. 2013). Apart from the family referred to above, the psyllids occurring in the Paleogene have been classified as members of three other families: Calophyidae, Carsidaridae and Psyllidae (Becker-Migdisova 1985, Shcherbakov, Popov 2002). Since the Miocene, representatives of all extant families occur in the fossil fauna, with the exception of Homotomidae (Burckhardt, Ouvrard 2012). Becker-Migdisova (1985) also included Permian Pincombeidae Tillyard, 1922 and Protopsyllidiidae Carpenter, 1931 in the Psyllomorpha Becker-Migdisova, 1962, but Shcherbakov (2000) proved that the former are more related to Aphidomorpha Becker-Migdisova and Aizenberg, 1962 and the Protopsyllidiidae have been assumed to be a sister group of the entire Sternorrhyncha Amyot and Serville, 1843 suborder (Grimaldi 2003; Grimaldi, Engel 2005). Currently, against earlier assumptions, they are not deemed to be direct ancestors of Psylloidea (Klimaszewski 1995, 1996, 1997a, b, c, d).

As provided by Ouvrard et al. (2010), the knowledge of the morphological structure of the fossil fauna representatives allows the researchers to correctly polarize characters in phylogenetic analysis. Harbach and Greenwalt (2012) stated that paleontological data also informs about the differentiation of morphological and anatomical structures occurring in time and helps to date individual lineages. In many cases, the condition of the preserved fossils hinders or renders impossible the observation of morphological structures that are important from the taxonomical point of view. Besides that, in case of psyllids the descriptions of extinct species, as it is in the case of extant insects, usually give no attention to the description of the thorax. Information on the structure of thorax, if present, is often incomplete and usually concern the shape of the prothorax plates located by the head.

Among the descriptions of psyllids of the Mesozoic, there is only one detailed description of the thorax of the *Liadopsylla apedetica* Ouvrard, Burckhard, 2010 from the family Liadopsyllidae, unfortunately, however, it lacks graphical documentation (Ouvrard et al. 2010). In the opinion of the authors mentioned, a representative of the Mesozoic Liadopsyllidae is characterized by a large prothorax, while the mesothorax and metathorax were as large as the prothorax. The propleurites (*proepimerum*, epm1; *proepisternum*, eps1) are long, dorsoventrally elongated and rectangular. The propleural sulcus (*sutura propleuralis*, pls1) is poorly visible, while the pleural apophysis is not visible. The prosternum (*prosternum*, st1) is extended. The perytrema (*mesothoracis peritrema*, ptm2) is located between the

pro – and mesothorax, although it is hardly visible. The mesothorax is large, with the parapteron (*parapterum*, ppt) situated before the tegula (*tegula*, tg). The mesopleurites (*mesoepimerum*, epm2; *mesoepisternum*, eps2) exhibit comparable dimensions and are vertically separated by the mesopleural sulcus (*sutura mesopleuralis*, pls2). A well visible pleural apophysis is located at the base of the pleural sulcus. The mesepisternum is divided by an anapleural cleft (*sutura anapleuralis*, acl2) into the dorsal anaepisternum (*anepisternum*, aeps) and the ventral katepisternal complex. The trochantinal apodeme (*fossa apodemae trochantinalis mesothoracis*, ftna2) is present and well visible. The transepimeral sulcus (*sulcus transepimeralis*, tems) is well visible and forms an external vertical convexity. At the ventral side, a large basisternum (*basisternum*, st2) with small internal furcae may be observed. The metathorax peritreme (*metathoracis peritrema*, ptm3) is well visible at the metathorax, while the spiracle is not visible. The metepisternum (*metaepisternum*, eps3) is large and separated from the katepisternal complex with an anapleural cleft (*sutura anapleuralis*, acl). The trochantin (*trochantinus metathoracis*, trn3) in the front of the mesocoxa is absent. The metepimeron (metaepimerum, epm3) is relatively large and separated from the metepisternum with a deep vertical metapleural sulcus (*sutura metapleuralis*, pls3) at the base of which, the metapleural apophysis is present. The metacoxa (*metacoxa*, cx3) is smaller than the mesocoxa (*mesocoxa*, cx2), less dorsally developed and freely articulated with the metapleurae at the dorsal side. The metacoxa (cx3) does not contain a developed meron that would increase the surface for the attachment of muscles responsible for jumping. The meracanthus (*meracanthus*, mcs) is very small.

In the opinion of some authors (Ouvrard et al. 2010), the morphology of this species, and especially the lack of apical spurs in the metatibia, the lack of enlarged metafemora and no changes in the structure of the metacoxa and metathorax – typical to extant psyllids – indicates unequivocally that the psyllids included in the Liadopsyllidae family of the Mesozoic were not capable of jumping.

The species of psyllids that lived in the Eocene do not exhibit a structure different to that of the extant psyllids and are ascribed to contemporary taxa. Information on their thorax, exceeding the descriptions of prothorax, have only been included in several works (Klimaszewski 1995, 1996; Drohojowska 2011) and until this day are only partial due to the poor condition of specimens.

The description of the thorax of *Eogyropsylla sedzimiri* Drohojowska, 2011 species of the family Aphalaridae (Fig. 67) is the most comprehensive. The species is characterized by a strongly declined head (between 45–90°) and a slightly arched dorsal margin of the thorax. No setae are visible on the thorax and no membranous area is observed between the head and the thorax. The pronotum (*pronotum*, nt1) is a plate slightly wider than the head with eyes and the anterior margin is slightly arcuate. Both in the central part and at the lateral margins, the pronotum is similar in length. In the dorsal view of the lateral parts, slight incisions might be observed, while no displacement of the lateral parts towards the head is observed. The posterior margin of the pronotum is arched and does not contain any incisions. The pronotum is not oblique in relation to the longitudinal axis of the body and is not covered by the head. The mesopraescutum (*mesopraescutum*, psc2) is narrower than the pronotum, reaching less than three times the length of the pronotum in the longitudinal axis. The mesopraescutum is 2.5 times wider than its length and visibly separated from mesoscutum with a slightly arched incision. In the dorsal view, the mesoscutum (*mesoscutum*, sc2) is a plate 2 times wider than its length and slightly longer than the mesopraescutum. The separation between the mesoscutum and the mesoscutellum is distinct and well visible. The mesoscutellum (*mesoscutellum*, scl2) is diamond-shaped, over 2.5 times larger than the mesoscutum and without any incision at the posterior margin. The mesopostnotum (*mesopostnotum*, pnt2) is situated behind the mesoscutum, covered by the mesoscutellum at the dorsal side and not visible. It runs as narrow diagonal strips towards the episternal sclerites. Both the parapteron (*parapterum*, ppt) and

the tegula (*tegula*, tg) are oval and comparable in terms of size. The metascutum (*metascutum*, sc3) is narrow, containing a wide metascutellum (*metascutellum*, scl3) elevated over the metascutum plate. The metapostnotum (*metapostnotum*, pnt3) is diamond-shaped and seems to be joining the first abdominal tergite.

The thorax of fossil species of the Psyllidae family is characterized by a pronotum (*pronotum*, nt1) that is slightly narrower than the head, proepisternum (*proepisternum*, eps1) and proepimeron (*proepimerum*, epm1) of the same size as well as a propleural sulcus (*sutura propleuralis*, pls1) reaching the central point of the lateral margin of the pronotum (Klimaszewski 1996, 1997). The thorax of *Succinopsylla dominikana* (Klimaszewski 1995), placed as a member of the Triozidae, on the other hand, is characterized by a pronotum (*pronotum*, nt1) with the anterior margin strongly curved towards the head and a nearly straight posterior margin. Besides that it also contains a wide and arcuate mesoscutum (*mesoscutum*, sc2) which is approximately 1.6 times wider than the mesopraescutum (*mesopraescutum*, psc2). The mesoscutellum (*mesoscutellum*, scl2) does not overlap the mesoscutum and is 3 times narrower than the mesoscutum. Information regarding the thorax morphology of remaining fossil species has not been presented in descriptions.

The current knowledge of the thorax morphology of fossil species is too incomplete to conduct a full study of the phylogeny of the fossil taxa. Such information may, however, be applied in the evaluation of the direction of changes in particular characters.

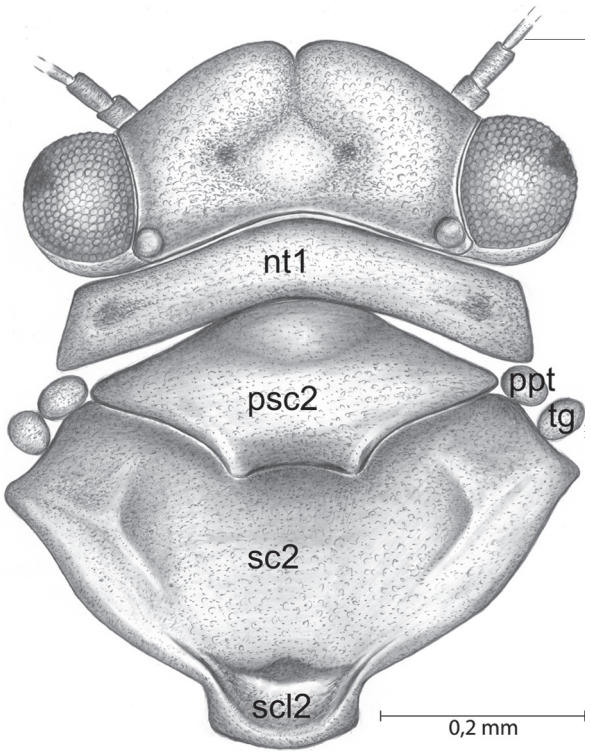


Fig. 67. *Eogyropsylla sedzimiri* Drohojowska, 2011 – dorsal side, after Drohojowska 2011

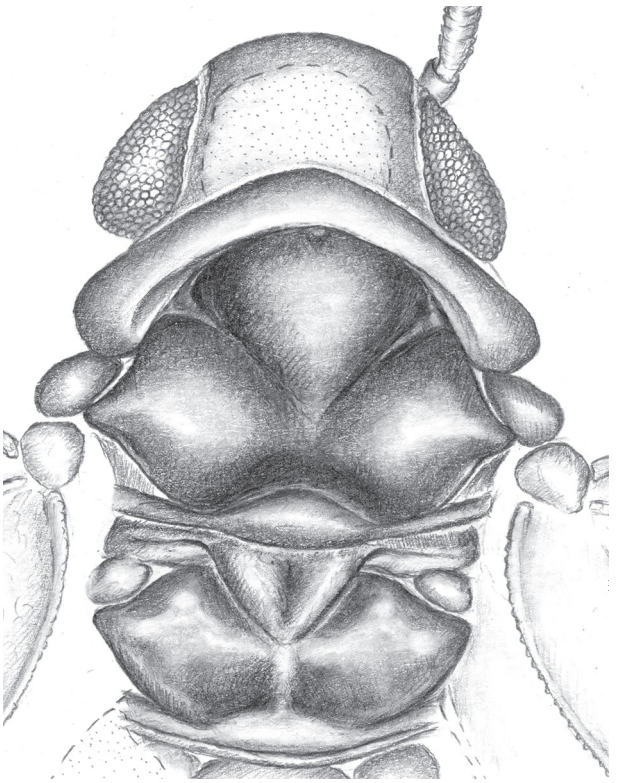


Fig. 68. *Paernis gregorius* Drohojowska and Szwedo, 2011 – dorsal side, after Drohojowska, Szwedo 2011, modified

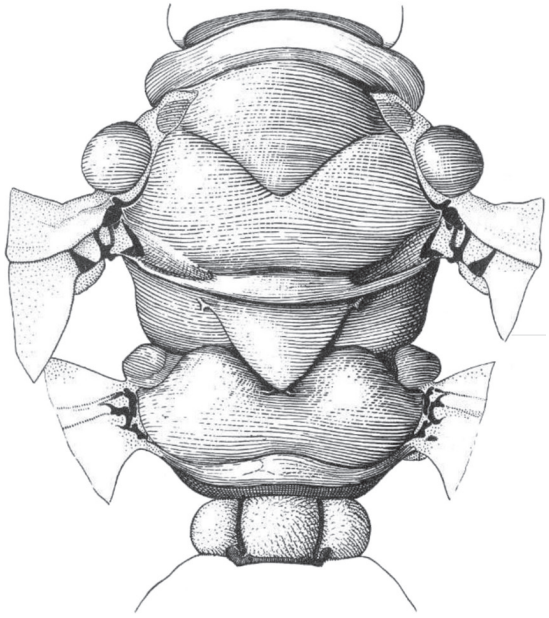


Fig. 69. *Aleyrodes proletella* (Linnaeus, 1758) – dorsal side, after Weber 1935, modified

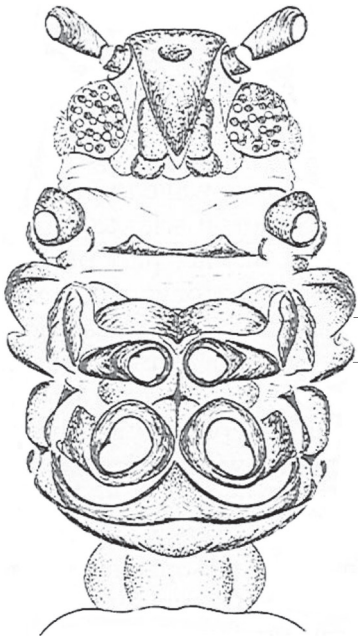


Fig. 70. *Aleyrodes proletella* (Linnaeus, 1758) – ventral side, after Wegierek 2002, modified

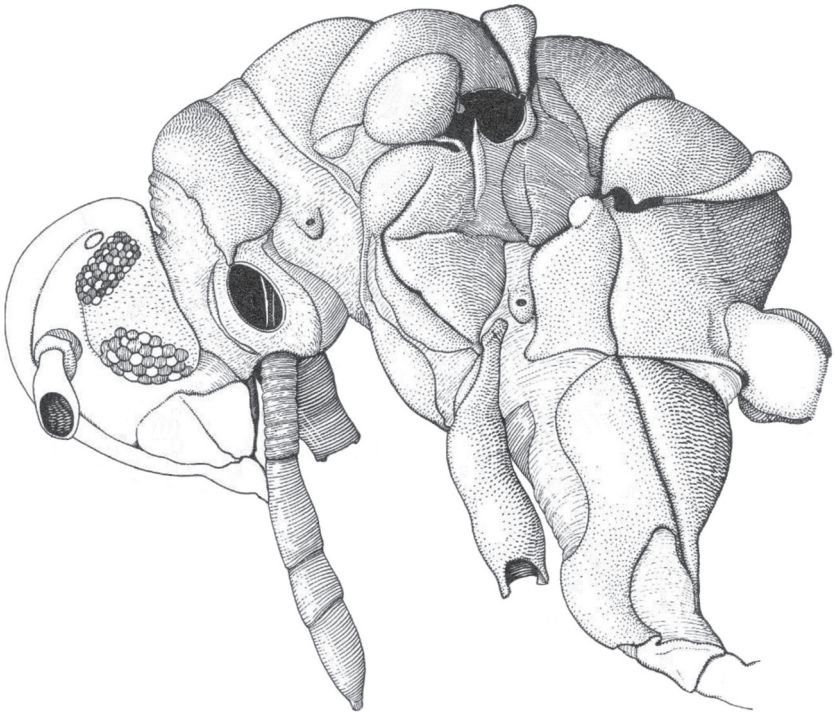


Fig. 71. *Aleyrodes proletella* (Linnaeus, 1758) – lateral side, after Weber 1935, modified

| Taxon \ Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 |
|---|---|---

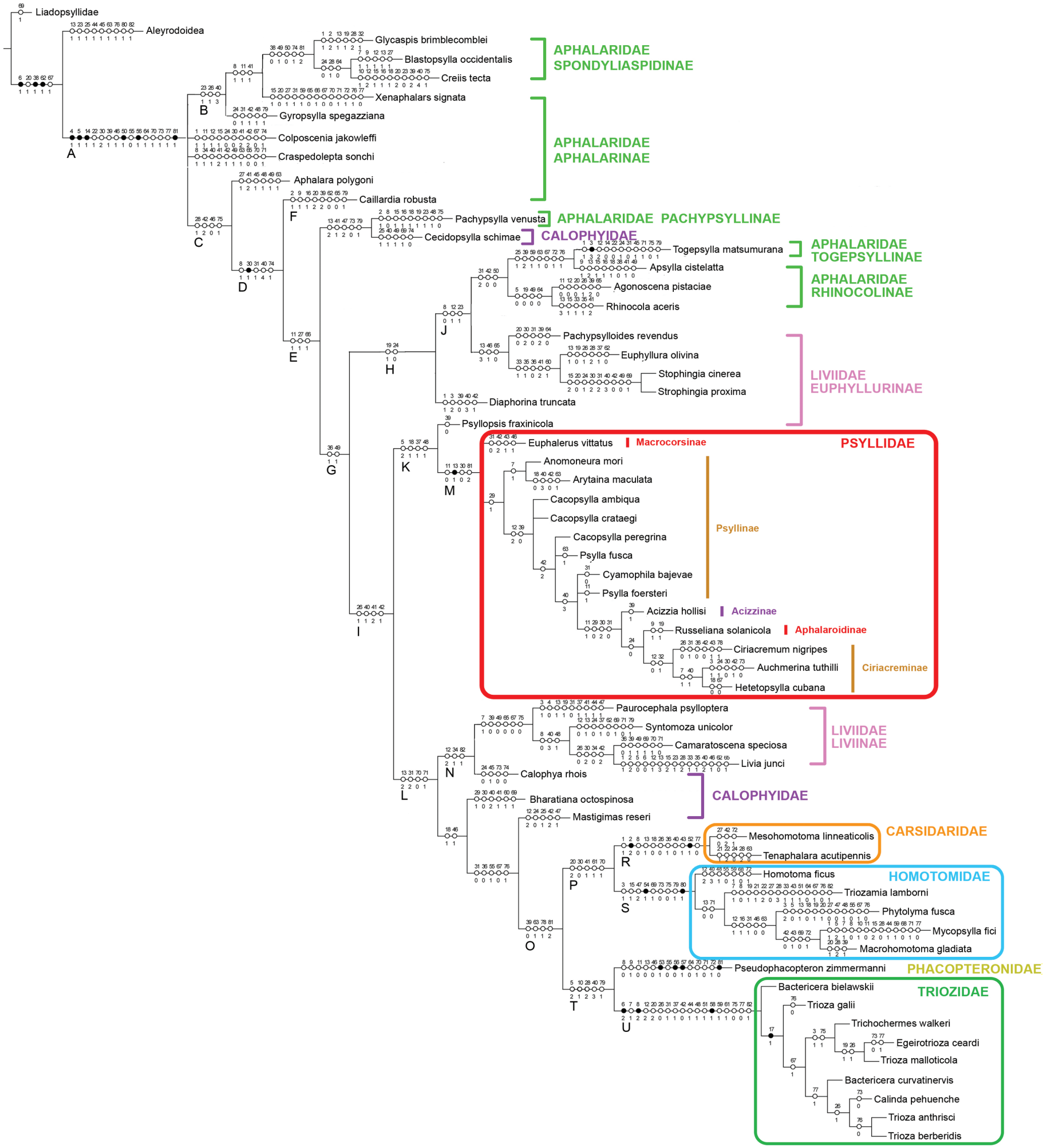


Fig. 73. Majority rule consensus tree. Black circles correspond to synapomorphies, white circles to homoplasies; numbers for characters correspond to those used in Tables 3, 4 and the text

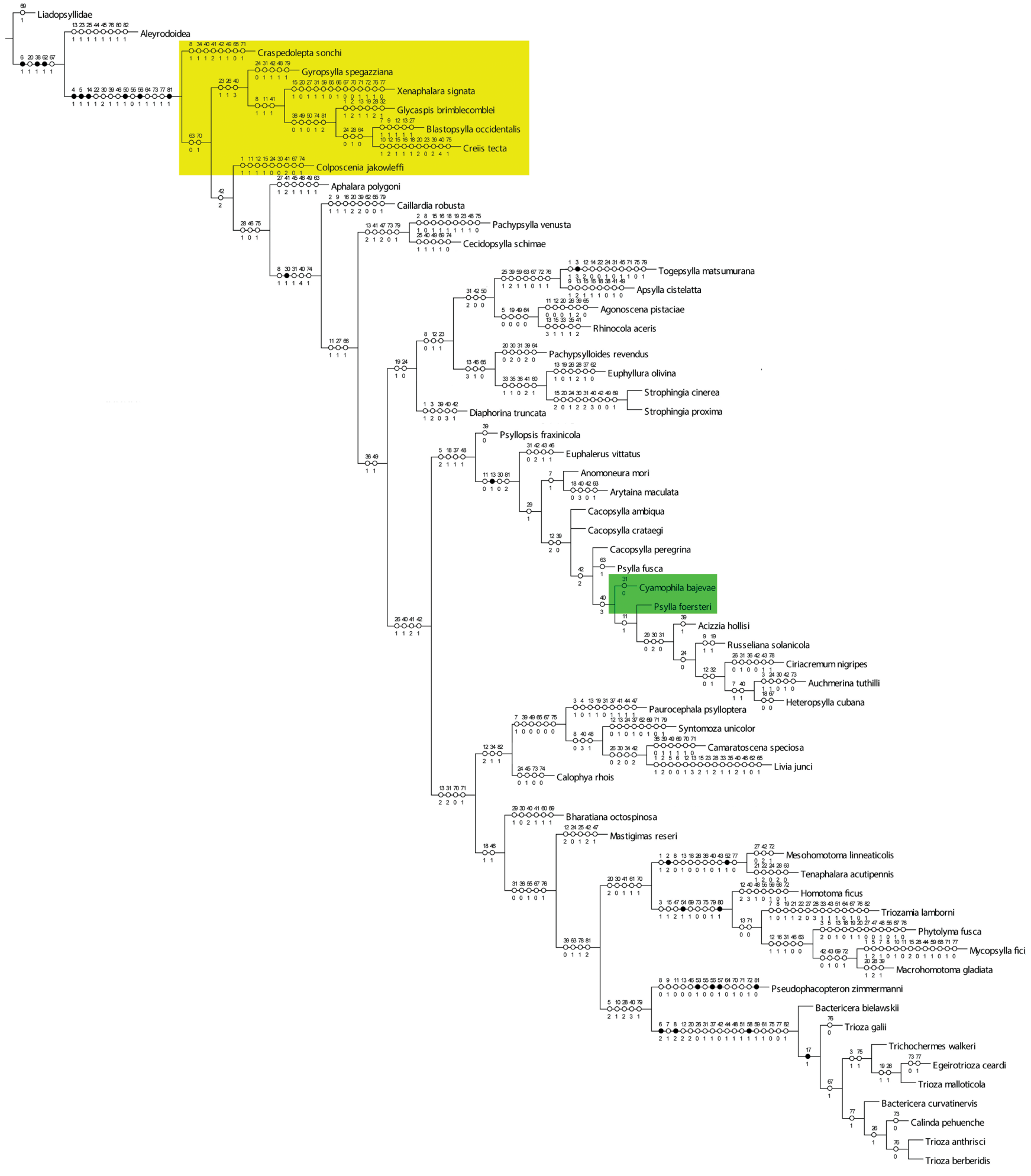


Fig. 74. Most parsimonious tree 1 received from TNT (Traditional Search algorithm) analysis. Black circles correspond to synapomorphies, white circles to homoplasies; numbers for characters correspond to those used in Tables 3, 4 and the text

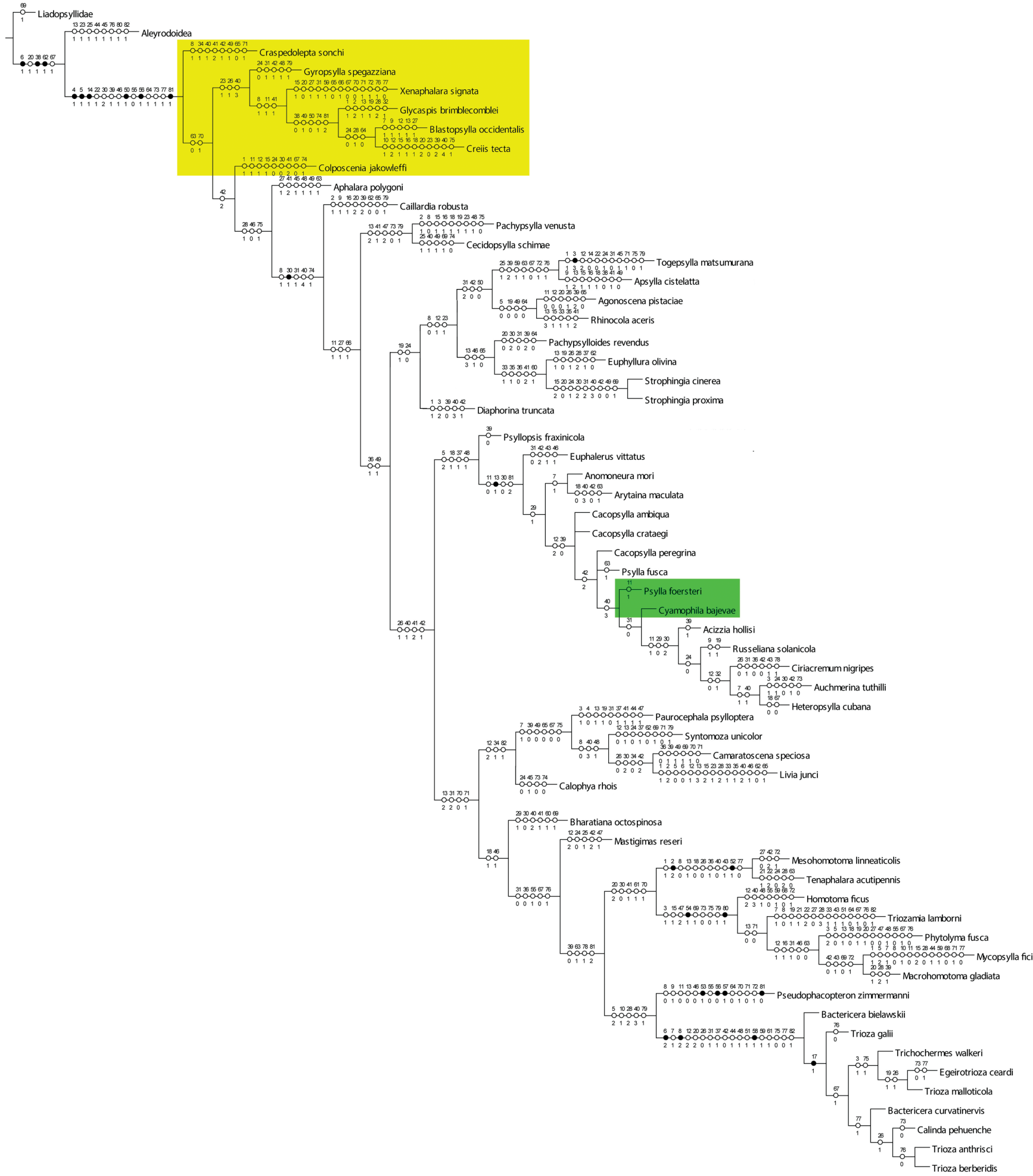


Fig. 75. Most parsimonious tree 2 received from TNT (Traditional Search algorithm) analysis. Black circles correspond to synapomorphies, white circles to homoplasies; numbers for characters correspond to those used in Tables 3, 4 and the text

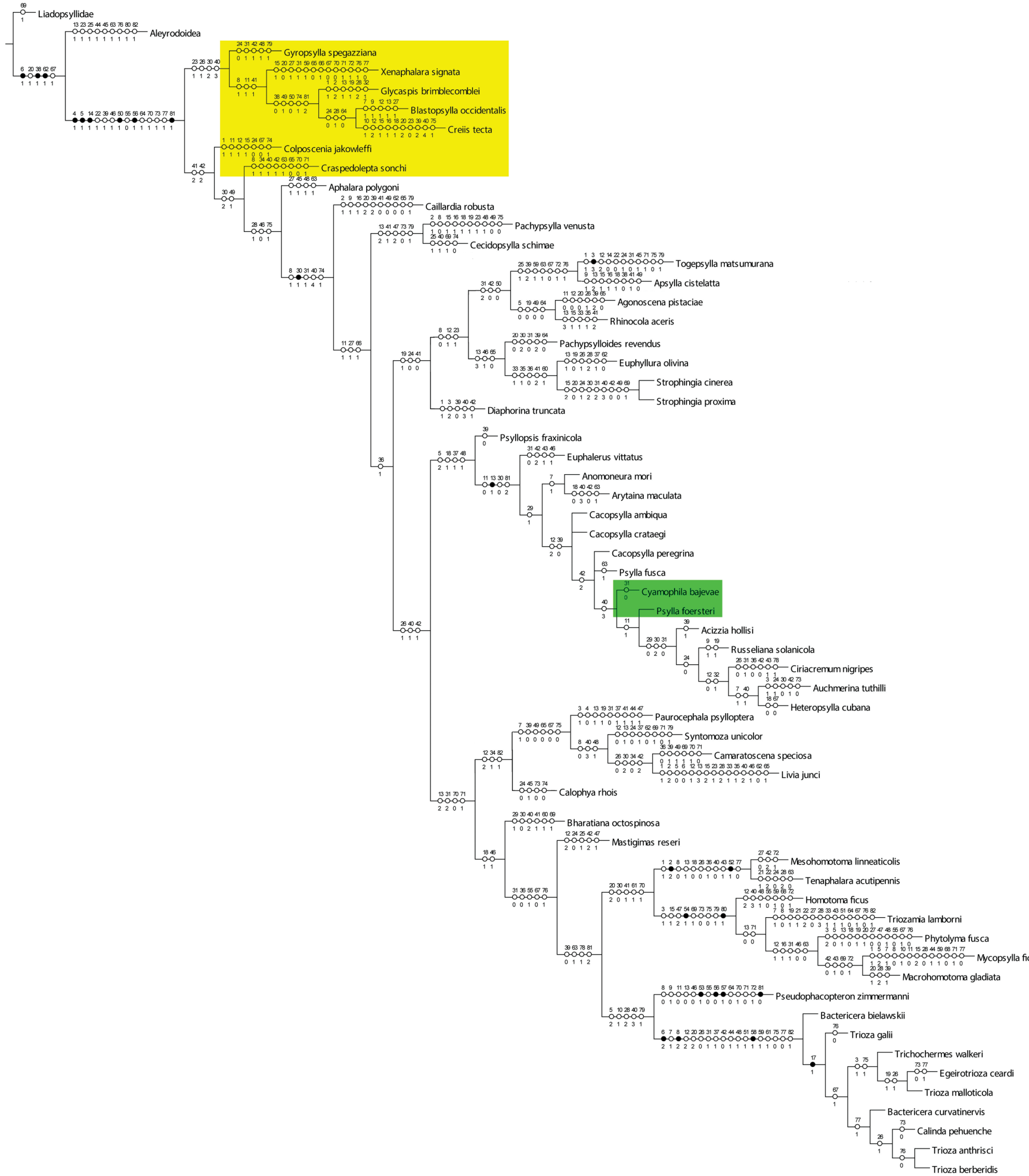


Fig. 76. Most parsimonious tree 3 received from TNT (Traditional Search algorithm) analysis. Black circles correspond to synapomorphies, white circles to homoplasies; numbers for characters correspond to those used in Tables 3, 4 and the text

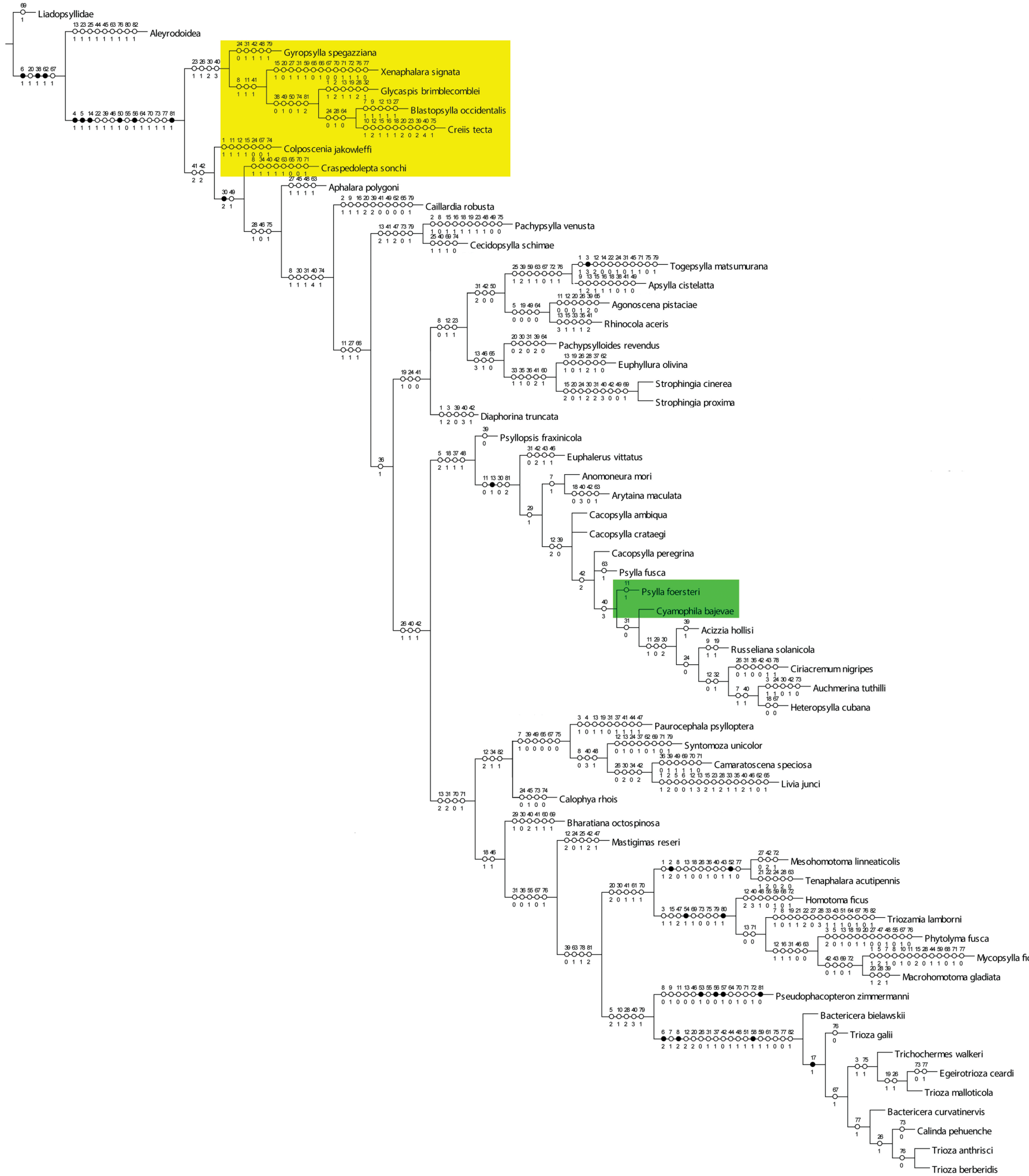


Fig. 77. Most parsimonious tree 4 received from TNT (Traditional Search algorithm) analysis. Black circles correspond to synapomorphies, white circles to homoplasies; numbers for characters correspond to those used in Tables 3, 4 and the text

3 Relationships within psyllids

3.1. An analysis of the direction of changes in the skeleton of psyllids

The directions of changes in the morphology of thorax in psyllids have been analyzed based on the following criteria: paleontological evidence and ingroup as well as outgroup comparisons.

The Aleyrodoidea superfamily (the sole family of infraorder Aleyrodomorpha Chou, 1963) has been selected as the outgroup. It is one of 4 recent infraorders distinguished within the Sternorrhyncha suborder (besides Aphidomorpha Becker-Migdisova and Aizenberg, 1962, Coccidomorpha Heslop-Harrison, 1952 and Psyllomorpha Becker-Migdisova, 1962). The relations between the individual units are still a subject of many paleontological studies and morphological comparisons, as well as molecular analyses (Schlee 1969a, b, c; Hennig 1981; Shcherbakov 1983, 1990, 2000, 2005, 2007; Shcherbakov, Popov 2002; Gullan, Martin 2003; Grimaldi, Engel 2005; Forero 2008). In view of the morphological data, Aleyrodoidea is a group that is most often regarded as a sister group of the Psylloidea (Quaintance, Baker 1913; Schlee 1969a, b, c; Popov 1980, 1981; Shcherbakov 1983, 2007; Klimaszewski, Wojciechowski 1992). Moreover, the highest similarity of thorax morphology between jumping plant-lice and whiteflies in the entire Sternorrhyncha has been earlier suggested by Crawford (1914) and Matsuda (1970). Besides the indicated close relationship between psyllids and whiteflies, the availability of works regarding their thorax, both in case of extant and extinct species, constituted an additional argument for the selection of this group. The description of this part of body in extant whiteflies has been provided by Weber (1931) and Węgierek (2002) in their analyses of the *Aleyrodes proletella* (Linnaeus, 1758) (Figs. 69–71) species, while the morphology of various extinct species has been given in the works of Drohojowska and Szwedo (2011a, b, 2013a, b, 2015) (Fig. 68).

In all species, the thorax is the largest and most scleritized tagma of the body. The thorax is directly joined with the head, which is declined to a various extent in relation to the main axis of the body **[1]** **(Numbers in bold provided in square brackets relate to characters used in the creation of the cladogram included in Tables 3 and 4. All discussed characters have been illustrated below**. In psyllids, the angle between the main axis of the body and the head is usually 45–90° **[1(0)]**. This character has been used in earlier analyses (Burckhardt, Lauterer 1989; Burckhardt, Mifsud 2003), and the polarization of this character was determined in the analysis of psyllid species trophically related only to the Verbenaceae (Burckhardt 2008) plants family.

The thorax in psyllids is curved to a variable degree **[2]**. This character is most easily evaluated by observing the side view of the dorsal margin of the thorax tergites. Extinct species of the Liadopsyllidae family (Becker-Migdisova 1985, Ouvrard et al. 2010) are characterized by a slightly curved thorax **[2(0)]**, as it is in the

case of other extinct species of the *Eogyropsylla* genus of the Aphalaridae family (Klimaszewski 1997c, Drohojowska 2011, Ouvrard et al. 2013). The gentle, slightly arcuate curve of the thorax has been regarded as a plesiomorphic state of that character. According to Klimaszewski (1964, 1979), the thorax of psyllids is slightly arcuate with a tendency to become more acute [**2(1)**]. Whereas the straightening of the thorax [**2(2)**], as in the genus *Livia* Latreille, 1802, has been forced by the specific transformation of the head, which rests against the pronotum at its entire width and is an apomorphic character (Klimaszewski 1964, 1979). Within this character, the changes proceeded in two directions – one is the progressive curving of the thorax, while the second is a straightening tendency to support the wider and more massive head. Hollis (1973, 1976) assumed that a slight curvature of the thorax is typical to the species of Psylloidea.

In all species of psyllids with developed genal cones they are always covered with shorter or longer sensory setae, while the rest of the body is usually smooth, without any setae [**3(0)**]. In several cases the body is covered with setae distributed on the head and thorax. These structures are usually sparsely distributed and delicate [**3(1)**], as in the case of *Triozamia lamborni*, *Homotoma ficus*, *Mycopsylla fici*, *Auchmerina tuthilli* and *Trichochermes walkeri*. Often the setae are short – their length is lower than the distance between individual seta (Olivares, Burckhardt 1997). The only analyzed species in which the entire thorax is densely covered with small setae is the *Diaphorina truncata* [**3(2)**]. On the other hand, the only species the head and thorax of which is covered with rigid and thick spurs is the *Togepsylla matsumurana*. In extinct species of psyllids, no setae on the thorax are observed (Klimaszewski 1993a, b, c, 1995, 1996, 1997a, b, c; Ouvrard et al. 2013; Drohojowska 2011). No setae are also observed in extinct whiteflies (Drohojowska, Szwedo 2011a, b, 2013a, b, 2015) or extant whiteflies (Weber 1931, 1995; Martin 2007). Within that character, two development directions may be distinguished: one is the increased density of setae on the body and the second is the formation of thick long setae resembling spurs.

As provided by Heslop-Harrison (1951), Ouvrard et al. (2002), Drohojowska (2009a, b, 2013), no additional sclerites are present in psyllids between the head and the pronotum, which was earlier suggested by Taylor (1918) and Weber (1929). In concordance with Ouvrard et al. (2002), the lack of these sclerites is an apomorphic character. In the presented study conducted with the use of SEM microscopy, no sclerites have been found between the head and the prothorax. The head and pronotum adjoin each other tightly in all analysed species [**4(1)**] with the exception of *Paurocephala psylloptera*, in which a membranous area is present between these two tagmata [**4(0)**]. It is possible that the cervical sclerites were gradually substituted with membranous formations which have also disappeared over time, causing the head to directly touch the pronotum. According to Snodgrass (1927, 1935), in the prothorax area of whiteflies there are three little sclerites, but they exhibit a tendency to blend, while Weber (1935, 1995) provides a description of a membranous area with a pair of vestigial sclerites interpreted by the author as cervical.

Klimaszewski (1964, 1979) regarded the massive pronotum, the width of which is similar to the width of the head, as a plesiomorphic state [**5(0)**]. It is gradually narrowing [**5(1)**]→[**5(2)**] in relation to the width of the head, along with the bending of the anterior margin [**6(0)**]→[**6(1)**]→[**6(2)**]. Also the shape of the entire sclerite changes and the direction of changes runs from the pronotum in the form of a collar, the length of which is similar at the central part and lateral sides [**7(0)**] and is broadened or narrower in the central part [**7(1)**]. A sclerite of a regular length, observed in all described extinct species, has been established as the plesiomorphic state of that character. Also the posterior, slightly arcuate edge of the pronotum without the central incision [**9(0)**] has been regarded as a plesiomorphic state.

Along the curvature of the pronotum, more distinct cavities are observed in the lateral parts of the tergite, from nearly invisible [**8(0)**],

through distinct cavities without posterior dislocations of a part of the pronotum towards the head [**8(1)**], to distinct incisions and distinct displacement of lateral parts in the direction of the head [**8(2)**].

In the side view, the pronotum is usually not covered or masked by the head [**10(0)**]. It is true for the extinct species of psyllids, and thus such state has been regarded as a plesiomorphic character, while the vertical arrangement and partial or total covering of the pronotum by the head has been assumed to be an apomorphic character [**10(1)**]. This character has been earlier used in cladistic analysis by White and Hodkinson (1985), who have also determined the polarization of the character.

Most often, the proepisternum (*proepisternum*, eps1) and the proepimeron (*proepimerum*, epm1) are plates characterized by similar dimensions [**11(0)**]. Such a state is observed in most extant species, but also in the case of extinct species (Klimaszewski 1996, 1997; Drohojowska 2011; Ouvrard et al. 2011, 2013) and it has been described as a plesiomorphic character. The propleural sulcus (*sutura propleuralis*, pl1) separating these pleurites in Liadopsyllidae (Ouvrard et al. 2010), Psyllidae (Klimaszewski 1996), Triozidae (Klimaszewski 1995) and Aphalaridae extinct species (Klimaszewski 1997c; Drohojowska 2011; Ouvrard et al. 2013) and in most extant species, runs vertically towards the top and reaches the centre of the lateral margin of the pronotum [**12(0)**]. Such a state has been classified as plesiomorphic. The direction of changes within that character consists in the displacement of the sulcus to the anterolateral angle of the pronotum [**12(1)**] or the posterolateral angle of the pronotum [**12(2)**]. When the propleural sulcus reaches the central region of the lateral margin of the pronotum, the propleurites are situated vertically and are usually wide [**13(0)**], as in the case of some of the extinct representatives of psyllids (Klimaszewski 1996). The subsequent stage of the changes in that character is the narrowing of propleurites, although they are still situated laterally and vertically [**13(1)**]. Subsequently, the propleurites are displaced in the anteroventral direction [**13(2)**] or in the ventral direction only [**13(3)**]. That character has been used earlier in cladistic analysis by Burckhardt and Basset (2000). Among all the analyzed species of psyllids, only in one case, the prosternum (*prosternum*, st1) is visible [**14(0)**] – in the case of *Togepsylla matsumurana*. In remaining cases, the area of the prosternum is covered by the rostrum and the first pair of legs [**14(1)**]. The covering of prosternum is related to the displacement of the mouthparts towards the back of the body and the partial connation of the labium with the ventral side of the prothorax. The head of the *Togepsylla* is situated nearly vertically in relation to the main axis of the body. This is why in the dorsal view, the posterior margins of the head and the pronotum touch each other and the membranous area is invisible, while in the lateral view it appears that a membranous area is present between the head and the thorax propleurites. One may assume that, as in the case of the membranous area visible between the head and the pronotum [**4**] in the dorsal view of *Paurocephala psylloptera*, it is an intermediate stage between the visible prosternum (in all insects classified as Sternorrhyncha) and the stage in which it is covered – as in all remaining psyllids. The prosternum was presented and described earlier (Weber 1929; Matsuda 1970; Journet, Vickery 1978). The works, however, always included diagrams instead of photographical documentation. It may be assumed that only the mounting of specimens will allow to make the prosternum visible.

Three sclerites have developed in psyllids, located between the prothorax and the mesothorax [**15**]. In nearly all descriptions of the thorax of psyllids, the peritreme (ptm2, *mesothorcic peritrema*) (Stough 1910; Brittain 1922; Tremblay 1965; Taylor 1918; Journet, Vickery 1978; Ramirez-Gomez 1955; Matsuda 1970) has been indicated, as it is the easiest to separate. Crawford (1914) and Brittain (1922) suggested that the anterior additional sclerite (*scleritum accessorium anterior*, aas) has separated from the dorsal part of the peritreme surrounding the spiracle. The studies of muscle courses have not, however, confirmed this claim (Ouvrard 2002). Most of the authors

who have characterized the thorax of the psyllids have classified this sclerite as an additional rectangular sclerite (Stough 1910; Crampton 1914a; Tremblay 1965; Matsuda 1970; Journet, Vickery 1978). The additional posterior sclerite (*scleritum accessorium posterior*, pas) was described as the one situated above the rectangular sclerite (Crampton 1914a; Crawford 1914; Taylor 1918; Brittain 1922; Tremblay 1965; Matsuda 1970; Journet, Vickery 1978). Among extant psyllids, usually all three sclerites are visible **[15(0)]** and the state of this character has been determined as plesiomorphic.

In extinct species of psyllids and in most extant species, the mesopraescutum (*mesopraescutum*, psc2) is narrower than the pronotum (Klimaszewski 1997a, b, c, d, Drohojowska 2011). That state of the character has been regarded as plesiomorphic **[16(0)]**.

Klimaszewski (1964, 1979) stated that the mesopraescutum in psyllids exhibits a narrowing and extending tendency in the direction of the head. From a wide and short fusiform plate **[17(0)]**, the mesopraescutum changes into a plate characterized by a similar length and width **[17(1)]**, and subsequently it gradually extends **[17(2)]**. Due to the extension, the mesopraescutum displaces the middle part of the pronotum and causes it to bend into an increasingly angled arc. Due to these modifications, changes in the length ratios of the pronotum and the mesopraescutum occur **[18]**. The change proceeds from the state in which the pronotum is up to three times the length of the mesopraescutum **[18(0)]**, up to the state of an increased ratio, in which the mesopraescutum is more than three times longer than the pronotum **[18(1)]**. The individual parts of the mesonotum (mesopraescutum, mesoscutum and mesoscutellum) are well visible in the fossil material and their boundaries are distinct. Such a clear separation of individual parts of the mesonotum and well developed sutures: the posterior mesopraescutum suture (*sutura mesopraescuti posterior*, pscs) **[19(0)]** and the mesoscutum suture (*sutura mesoscuti*, scs) **[26(0)]** may be considered as primitive characters. As provided by Klimaszewski (1964, 1975, 1979), along the gradual enlargement of the mesoscutum, the size of its anterior incision **[20]**, where the mesopraescutum is inserted, increases. The straight anterior margin of the mesoscutum has been regarded as the plesiomorphic state **[20(0)]** (Klimaszewski 1964, 1979).

The gradual broadening of the mesoscutum results in the changes of the ratios between the individual parts of the mesoscutum. The width of the mesoscutum is usually twice its length **[21(0)]**, but these proportions vary. In extinct species of the Aphalaridae family, the width of the mesoscutum is over twice its length, so this character has been classified as plesiomorphic (Klimaszewski 1997c, Drohojowska 2011). Also the F/G ratio (Fig. 4) undergoes changes. The ratio concerns the length of the mesoscutum in the midline and the length of the lateral sides of that plate **[22]**. In all analyzed extinct species, this ratio amounted to approximately 1, which allowed for classifying that state as plesiomorphic **[22(0)]**. In all the analysed extinct species of psyllids, the mesoscutum is as long as or slightly longer than the mesopraescutum **[23(0)]**, while the mesoscutum is over 1.5 times wider than the mesopraescutum **[24(0)]**. Such proportions are also preserved in most of the extant species and have been described as plesiomorphic. In the mesoscutum **[25]** of extinct Aphalaridae family species (Drohojowska 2011) the H/G ratio (Fig. 4) amounts to approximately 2 – as it is in the case of nearly all extant species of psyllids – and this state has been classified as plesiomorphic.

In psyllids, the mesoscutellum (*mesoscutellum*, scl2) is a narrow plate **[27]** assuming various shapes **[28]**. In the fossil material, the mesoscutellum is usually rectangular **[28(0)]**, with no incision in the posterior margin **[29(0)]** (Klimaszewski 1996, 1997; Drohojowska 2011). Two directions of changes in the mesoscutellum may be described. One relates to the transformation of the rectangle into a wide trapezoid **[28(1)]**, which is subsequently narrowed **[28(2)]** due to the growth of the mesoscutum referred to earlier. The other relates to the bending of the rectangular mesoscutellum into an arcuate U-shaped structure **[28(3)]** due to the direction of the changes.

The mesopleural suture (*sutura mesopleuralis*, pls2) in psyllids has been described by many authors (Crawford 1914; Taylor 1918; Brittain 1922; Boselli 1928; Weber 1929; Tremblay 1965; Matsuda 1970; Journet, Vickery 1978). In psyllids, this suture always runs from the condyle of the coxa towards the centre of the pleuron and never touches the base of the wing, as it is in the case of other Pterygota. It is believed that such an incomplete development of the mesopleural sulcus is related to the poor flying capabilities of psyllids (Clark 1962). The visibility of that sulcus at the mesopleuron, its length and course are variable [**31**]. In Liadopsyllidae (Ouvrard et al. 2010), the sulcus is well visible, long and runs diagonally towards the top [**31(0)**]. The changes of that character had a bidirectional course – the first was the shortening of the sulcus and the decrease in its visibility [**31(1)**] and the second was the increasingly vertical course of that sulcus [**31(2)**].

The second mesothoracic suture – the anapleural cleft (*sutura anapleuralis*, acl2) is well visible, long and horizontal [**31(0)**] in Liadopsyllidae and most extant species. Such a form of this suture has been classified as plesiomorphic. The direction of changes within this character leads towards the shortening of this suture, its diagonal situation and almost to its disappearance [**31(2)**]. The suture has been earlier described by Weber (1929) and Matsuda (1970, 1979), although its course had been described incorrectly.

In some species, the mesopleural sulcus (*sutura mesopleuralis*, pls2) and the anapleural cleft (*sutura anapleuralis*, acl2) may touch each other, but it is undoubdtedly an apomorphic character [**32(1)**], as no such touching of these parts is found in the fossil record of that group or any other group within the Sternorrhyncha.

The parapteron (*parapterum*, ppt), described earlier by many researchers (Stough 1910; Crawford 1914; Taylor 1918; Brittain 1922; Boselli 1928; Weber 1929; Tremblay 1965; Matsuda 1970) is usually an oval structure [**33(0)**], both in extant species and in all known extinct species. The same concerns the tegula (*tegula*, tg) [**35(0)**], the description of which is also found in numerous works (Taylor 1918; Brittain 1922; Boselli 1928; Weber 1929; Tremblay 1965; Matsuda 1970). It was thus decided that the oval shape of both the structures is their plesiomorphic state. In the analyzed fossil material, the parapteron is always larger than the tegula [**34(0)**] and – with a few exceptions – the same concerns the extant fauna. It has been determined that the larger size of the parapteron is a plesiomorphic character.

Part of the researchers interpreted the transepimeral sulcus (*sulcus transepimeralis,* tems) located at the mesothorax as the mesopleural sulcus (Matsuda 1970, 1979; Journet, Vickery 1978). Ouvrard et al. (2002), however, proved that the sulcus does not begin with the internal pleural apophysis as in the case of the pleural sulcus in each tagma and thus should be interpreted as an additional sulcus. In Liadopsyllidae, as well as in most of the extant species, the sulcus is distinct and well visible. Such a state has been classified as plesiomorphic [**36(0)**].

At the ventral side, anteriorly of the mesocoxa of some extant psyllid species, a convexity occurs, namely the trochantin tubercle. No such convexity is observed in extinct species of psyllids, so the existence of such a convexity is apomorphic [**37(0)**]. In line with the description by Journet and Vickery (1978), the proepisternum contains a dorsal extension, the so-called trochantin process, included also in the earlier works by Crawford (1914), Tremblay (1965) and Matsuda (1970).

In the extinct Liadopsyllidae species, as in most extant psyllids, the anterior margin of the mesosternum is straight and free of incisions. This state has thus been considered plesiomorphic [**38(0)**].

The pleurosternal suture (*sutura pleurosternalis*, pss) limiting the basisternum (*basisternum*, st2) is usually well visible in extant species [**39(0)**]. It is a plesiomorphic character and the gradual disappearance of that suture has been recognized as apomorphy. The formation of the pleural sulcus impacts the shape of the basisternum and usually the plate assumes a diamond-like shape [**40(0)**]. The changes in the shape of that plate proceed in three directions. The first direction is the transformation of the rhomboidal shape into an oval one [**40(1)**] and subsequently

into a shape of mushroom due to the incision in the posterior part [**40(2)**]. The second direction is the flattening of the anterior part of the rhomboidal plate, causing it to assume a triangular shape [**40(3)**]. The third direction is the gradual disappearance of the pleurosternal suture which renders impossible the determination of the shape of the basisternum [**40(4)**].

The width of the lateral parts of the katepisternum (*katepisternum*, kes2) that are visible on the ventral side may be equal to the width of the head. Such a state is usually observed in extant species of psyllids [**41(0)**], although it may also be slightly wider [**41(1)**] or narrower [**41(2)**] than the head. The anterior parts of the katepisternum are small and oval in shape in case of extinct species of the Liadopsyllidae family and most of the extant species [**42(0)**]. Such a state has been treated as plesiomorphic. The direction of changes within that character consists on one hand in the enlargement of the katepisternum towards the head while maintaining the oval shape [**42(1)**] and in the change of the shape from oval to pointed while maintaining the dimensions [**42(2)**] on the other.

In some of the extant species of psyllids, the mesoscutellum and metascutellum overlap with the metascutum (*metascutum*, sc3) which renders the metascutum invisible from the dorsal side [**43(1)**]. In extinct insects, the metascutum is always well visible and thus such a state of the character has been recognized as apomorphic.

The metascutellum (*metascutellum*, scl3) is usually a plate half the width of the mesoscutellum [**44(0)**] and shorter than the mesoscutellum [**45(0)**]. It was decided that such large disproportions of the metascutellum and the mesoscutellum are apomorphic states of these characters. Usually the metascutellum is also a rectangular plate [**46(0)**], which may assume a trapezoidal shape [**46(1)**].

No tubercles on the metapostnotum (*metapostnotum*, pnt3) are observed in extinct psyllids. Also in most extant species no such tubercles are observed on that part of the metathorax. Such a state of the character may be assumed to be plesiomorphic [**47(0)**]. In a few extant psyllid species, there is a single tubercle formed in the middle of the metapostnotum [**47(1)**], or two tubercles distributed symmetrically at both sides of the plate [**47(2)**]. No such structures are observed in any of the groups placed in Sternorrhyncha. The presence of tubercles at the dorsal part of the metathorax has been earlier suggested by Burckhardt and Mifsud (2003), who used this character in cladistic analysis. They proved the presence of a tubercle-shaped structure in the species of the genus *Paurocephala* Crawford, 1913 not on the metascutellum, as they suggested in the descriptions, but on the metapostnotum – which may be inferred from the photographs included by the authors and has been confirmed in the presented study.

In comparison to the trochantin of other Sternorrhyncha, the metathoracic trochantin (*trochantinus metathoracis*, trn3) in psyllids is a highly developed structure (Crawford 1914; Crampton 1909, 1914a, b; Brittain 1922; Matsuda 1970, 1979). This is related to the psyllids' unique capability to jump. Additionally, in some species of extant psyllids, three convexities are formed on the surface of the trochantin, which enlarge the area of the attachment of the muscles responsible i.e. for jumping. In Liadopsyllidae and Malmopsyllidae no convexities are present on the trochantin and following Ouvrard et al. (2010), they were not capable of jumping. In other Sternorrhyncha, also incapable of jumping, no convexities are present on the trochantin. It is thus a character that only occurs in some of the psyllids and as such, that state has been recognized as apomorphic [**48(1)**]. Apart form the highly developed trochantin, the transformations of the metathorax in psyllids also encompass the counterclockwise rotation of the metathoracic pleurites and their formation of a uniform elongated arc (Ouvrard et al. 2002). Such changes cause the metapleural sulcus (*sutura metapleuralis*, pls3) to be weakly visible [**49(0)**], in many psyllids and, most often, to disappear [**49(1)**]. In the opinion of Ouvrard et al. (2002), each of the three parts of the thorax: the prothorax, the mesothorax and the metathorax, evolved at a different pace and independently from the others. The structure of the prothorax may be

assumed to be the most primitive and the least changed. The propleural sulcus is fully developed and runs vertically. The structure of the mesothorax is more transformed in comparison to the prothorax and the mesopleural sulcus is not fully developed, usually running diagonally, sometimes vertically, and sometimes its absolute disappearance is observed. The metathorax is the most transformed part. The metapleural sulcus is visible only in a few species. It is always vestigial, situated nearly horizontally up to its absolute disappearance. Such independent evolution of the prothorax, mesothorax and metathorax has been earlier described in the work by Du Porte (1964), regarding the species of the Plecoptera. The formation of a large horn-shaped meracanthus (*meracanthus*, mcs) at the metacoxa (*metacoxa*, cx3) additionally facilitates the jumping capability of psyllids. No such structure is present in the Liadopsyllidae or the Sternorrhyncha suborder insects. It only appears in psyllids and as such, the character should be treated as apomorphic **[50(1)]**.

The remaining characters **[51–82]** used in the creation of cladograms concern the appendages of the thorax, namely the forewings and hindwings, as well as the legs of the third pair. These parts of the psyllid body have been described numerous times by various authors and most of the selected characters exhibit a specified polarization and was used in earlier cladistic analyses.

The main vein ($R+M+Cu_1$) branches into smaller veins right at the beginning of the wing and the radius vein usually branches as the first one, while the media and cubitus veins remain fused and branch only in a further part of the wing **[51(0)]**. Such a course of the veins is observed in all psyllid species except for the Triozidae family, in which all three veins branch from the main vein in the same point **[51(1)]**. In the extinct species of the Malmopsyllidae and Liadopsyllidae families, dichotomous branching of the main vein is observed (Becker-Migdisova 1985; Shcherbakov 1988; Klimaszewski, Wojciechowski 1992; Ouvrard et al. 2010). Such a dichotomous branching of the main vein has been recognized as the plesiomorphic state, while the trichotomous branching has been classified as apomorphic (Klimaszewski 1975; White, Hodkinson 1985).

The presence of the crossvein between the Rs and M veins **[52]** has been used in the cladistic analysis of species of the Rhinocolinae subfamily (Burckhardt, Lauterer 1989), the Homotomidae family (Hollis, Broomfield 1989) and the psyllids trophically related to the Zygophyllaceae (Burckhardt, Ouvrard 2006). The presence of the additional transverse vein has been considered autapomorphy by Klimaszewski (1975) **[52(0)]** and such polarization of the character was assumed by subsequent authors (Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt, Ouvrard 2006). The extinct species of the Liadopsyllididae and Malmopsyllidae families do not have the crossvein between the Rs and M veins (Becker-Migdisova 1985; Shcherbakov 1988; Klimaszewski, Wojciechowski 1992; Ouvrard et al. 2010).

Except for the Phacopteronidae family, in all species of psyllids the Rs and M_{1+2} veins run in parallel. A similar parallel course of the veins is characteristic to extinct species of the Malmopsyllidae and Liadopsyllidae families (Becker-Migdisova 1985; Shcherbakov 1988; Klimaszewski, Wojciechowski 1992; Ouvrard et al. 2010) and such a state has been regarded as plesiomorphic **[53(0)]** (Hollis 1987). The increase in the proximity of the Rs and M_{1+2} veins, observed in the species of the Phacopteronidae (Hollis 1987) is considered as apomorphy.

The presence and the length of the cubitus was used in the analysis of the Homotomidae family species (Hollis, Broomfield 1989). The authors have considered the presence of the long cubitus as the plesiomorphic state **[54(0)]**, while its shortening and final disappearance was considered to be apomorphic **[54(1)]**. A long cubitus is observed in most extant psyllids and in all extinct psyllids of the Malmopsyllidae and Liadopsyllidae (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard et al. 2010).

The presence of a costal break at the anterior margins of the wings in psyllids, or the lack thereof, has been used in many conducted analyses of adult insects (White, Hodkinson 1985; Hollis 1987; Hollis, Broomfield 1989; Burck-

hardt, Lauterer 1989; Burckhardt, Basset 2000). At the posterior margin of the wing, in the location of the sutura clavi, also a so-called anal break is observed, while between these breaks, some primitive species exhibit the presence of a nodal line. According to Klimaszewski (1975), the presence of both the anterior and the posterior break, as well as the nodal line are plesiomorphic characters **[55(0)]** and as such they have been used in the analyses made to that moment (White, Hodkinson 1985; Hollis 1987; Hollis, Broomfield 1989; Burckhardt, Lauterer 1989; Burckhardt, Basset 2000). The anterior break has not been described in the case of the Liadopsyllidae (Becker-Migdisova 1985, Shcherbakov 1988, Klimaszewski, Wojciechowski 1992, Ouvrard et al. 2010). On the other hand, the presence of the posterior break has been indicated by Klimaszewski and Wojciechowski (1992).

The marginal vein, which was formed as a result of merging of the costal and subcostal veins (C+Sc), is arcuate in most extant psyllids **[56(1)]**. Among all the analyzed species, a straight anterior margin of the wing **[56(0)]** may only be observed in the Phacopteronidae. The straight wing margin occurs in majority of extinct Malmopsyllidae and Liadopsyllidae (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard et al. 2010) and that state of this character has been regarded as plesiomorphic. The shape of the anterior margin of the wing has been used in analyses conducted by White and Hodkinson (1985).

The distribution of the breaks at the anterior and posterior margin of the wing and their distance from adjacent veins has not been used in cladistic analysis to that moment. Among the analyzed species, only the Phacopteronidae exhibits a costal break that is distant from the location where the vein R_1 reaches the margin of the wing. Such a state of the character has been classified as apomorphy **[57(1)]**. In all remaining analyzed species, the anterior break lies near the connection of the vein R_1 with the anterior margin of the wing and such a state has been considered as plesiomorphic **[57(0)]**. The location of the anal break close to the vein Cu_{1b} is a character present in most psyllids and thus it has been considered as plesiomorphic **[58(0)]**. Among the analyzed species, the increase in the distance of the anal break from the Cu_{1b} vein is exhibited only in the species of the Triozidae and such state has been recognized as apomorphic **[58(1)]**. In fossil material, the anal break is located near the vein Cu_{1b} (Becker-Migdisova 1985; Klimaszewski, Wojciechowski 1992).

In their analysis of the psyllids representing family Homotomidae, Hollis and Broomfield (1989) used the location where the vein M_{1+2} approaches the margin of the wing. They have considered the state in which the vein M_{1+2} reaches the margin of the wing behind its apex as plesiomorphic **[59(0)]**, while classifying the state in which the vein reaches the margin before the apex as apomorphic **[59(1)]**. The authors have not given consideration to the state in which the vein M_{1+2} reaches the margin of the wing exactly at the apex. Because no extinct species of the Malmopsyllidae and Liadopsyllidae exhibit the apomorphic state, although there are species in which the vein M_{1+2} reaches the margin of the wing both behind the apex and at the apex (Becker-Migdisova 1985; Shcherbakov 1988; Klimaszewski, Wojciechowski 1992; Ouvrard et al. 2010), both states have been classified as plesiomorphic **[59(0)]**.

Psyllid wings are usually the widest in the section between the half and 2/3 of their length, subsequently becoming narrower towards the apex. Such wing shape is typical to most species of extant families and the species of the Malmopsyllidae and Liadopsyllidae extinct families (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard et al. 2010). The broadening of the wings in the anterior, base part of the wing in extinct species has not been described yet and occurs rarely in extant species. Thus, it has been classified as an apomorphic character **[60(1)]**. The state in which the wings are the widest in the section between the half and 2/3 of their length has been considered as plesiomorphic **[60(0)]**, thus changing the polarisation of the character earlier used by Burckhardt and Ouvrard (2001) and assuming that the broadening of the wing in 2/3 of its length as plesiomorphic and

the broadening in the middle of the wing is apomorphic. The final stage of transformation has been described as the broadening in the 1/3 of the wing length.

The shape of the wings of psyllids was applied in the analyses conducted by Hollis (1984, 1987), who recognized the rounded ends of the wings as the plesiomorphic state **[61(0)]**, as opposed to wings ending with a more or less distinct apex **[61(1)]**. He has also determined that wide wings are a plesiomorphic character **[62(0)]** and narrow wings are an apomorphic character **[62(0)]**. Such a polarization of characters has been earlier suggested by Klimaszewski (1975). In all extinct species of the Liadopsyllidae and Malmopsyllidae described to the moment, the wings end with a slight, semicircular arc and are narrow (Becker- Migdisova 1985, Shcherbakov 1988, Ouvrard et al. 2010).

The presence of the pterostigma or the lack thereof in psyllid wings has been used in numerous cladistic analyses (White, Hodkinson 1985; Hollis 1987; Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt, Basset 2000). The presence of the pterostigma has been recognized as a plesiomorphic state **[63(0)]**, while its lack has been assumed to be apomorphic **[63(1)]**, as suggested earlier by Klimaszewski (1964, 1975). Becker-Migdisova (1985) and Shcherbakov (1988) provide no description of pterostigma in the Liadopsyllidae family species, while in the work by Ouvrard et al. (2010), the authors stated that the pterostigma is present in *Liadopsylla hesperia* Ouvrard, Burckhardt 2010 and visible only as a darker area of the wing. They also claimed that the pterostigma is barely visible in *L. apedetica* Ouvrard, Burckhardt 2010.

In all extinct species of the Liadopsyllidae and Malmopsyllidae, the marginal vein (S+Sc) is not broadened (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010). In most extant species, the marginal vein has assumed the same form and such a state has been classified as plesiomorphic **[64(0)]**. The broadened marginal vein occurs in some of the analyzed species classified as members of the families Aphalaridae, Homotomidae and Liviidae and has been regarded as an apomorphic character **[64(1)]**. This character was used by Burkhardt and Lauterer (1989) in their analysis.

In his cladistic analysis, Burckhardt (1991) used the ratios of lengths of individual veins of the forewings. He noted that the R vein is more or less the same length as the vein $M+Cu_1$ and such a state may be considered as plesiomorphic **[65(0)]**. The case in which the lengths of the veins are significantly different was regarded by him as apomorphy **[65(1)]**.

Apart from the comparisons of the lengths of the R and $M+Cu_1$ veins, Burckhardt (1991) also used the lengths of the $M+Cu_1$ and Cu_1 veins and noted that the state in which the length of the vein Cu_1 corresponds to the length of the vein $M+Cu_1$ is plesiomorphic **[66(0)]**. Comparing the lengths of these two veins among the extinct species of the Liadopsyllidae, both states of that character may be found. In all species of the Jurassic described by Becker-Migdisova (1985) and Shcherbakov (1988), the $M+Cu_1$ and Cu_1 veins are similar in sizes, while in the case of two younger species of the Cretaceous, described by Ouvrard and Burckhardt (Ouvrard et al. 2010), these veins notably differ in lengths. Similarly to most of the Liadopsyllidae, the vein lengths of all the Malmopsyllidae were similar, so is seems well founded to consider this character plesiomorphic **[66(0)]**, as proposed by Burckhardt (1991).

The shapes of the individual veins on the forewings, especially the Rs, M_{1+2} and Cu_{1a} have been used in cladistic analyses (Burckhardt, Basset 2000; Burckhardt, Ouvrard 2001). The shape of the vein Rs was used by Burckhardt and Basset (2000) in the analysis of psyllid species trophically related to *Schinus* spp. (Anacardiaceae). The vein Rs that was straight or curved towards the centre of the wing was considered by the authors as a plesiomorphic state **[67(0)]**, while regarding the vein curved towards the anterior margin of the wing as apomorphic **[67(1)]**. Extinct Liadopsyllidae species exhibit a curved vein Rs towards the centre of the wing or straight (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010). Burckhardt and Basset (2000) also used the curve

of the vein M_{1+2}, assuming that its curve towards the cell m_1 is plesiomorphic [**68(0)**] and regarding the curve in the opposite direction towards the margin of the wing as apomorphic [**68(1)**]. Among the Liadopsyllidae, the vein M_{1+2} is curved in both ways (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010), while in most extant psyllid species the vein M_{1+2} is curved towards the centre of the cell m_1. Burckhardt and Ouvrard (2001) used the shape of the vein Cu_{1a}, indicating that a delicate curve towards the centre of the wing is a plesiomorphic state [**69(0)**]. They have determined the direction of changes in the shape of that vein as a gradual decrease in the curve, that is towards a nearly straight course, until it finally becomes concave. As none of the analyzed species exhibited a concave vein Cu_{1a}, that state has not been considered in the polarization. The nearly straight course of the vein has been classified as the apomorphic state [**69(1)**].

Hollis (1984, 1987) established that the cell m_1 in the wing is a primary character [**70(0)**], while its reduction is an apomorphic character [**70(1)**]. The size of the cell m_1 has been used in the analysis conducted by Burckhardt and Basset (2000), but these authors assumed a polarization opposite to the one by Hollis. Because all the extinct species, both representing the Liadopsyllidae and Malmopsyllidae families, exhibit wings with a large cell m_1, similarly to most extant psyllids, such a state is considered as plesiomorphic in line with Hollis (1984, 1987).

Apart from the size, the shape of the cell m_1 has also been used in cladistic analysis. According to Burckhardt and Lauterer (1997), the narrow shape of the cell m_1 was plesiomorphic, namely the state in which the M_{1+2} and M_{3+4} veins reach the margin of the wing near each other. If the veins reach the margin of the wing in distant points, the character is considered as apomorphic [**71(0)**]. All extinct species of the Liadopsyllidae and Malmopsyllidae exhibit a narrow shape of the cell m_1 (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010). Besides the size and the shape of the cell m_1, Burckhardt (1986) also analyzed the size and shape of the cell r_1, assuming that its long and narrow shape is a plesiomorphic state [**72(0)**], while considering its shortening and expansion as the apomorphic state [**72(1)**]. In case of the extinct species of the Liadopsyllidae and Malmopsyllidae, the cell r_1 is long and narrow, with the exception of *Malmopsylla karatavica* Becker-Migdisova, 1985 (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010).

In all species of the families Liadopsyllidae and Malmopsyllidae, the length of the cell cu_1 is larger than its height, as in most extant psyllids. This character may thus be considered as plesiomorphic [**73(0)**]. When the cell cu_1 height is significantly larger than its length, the state may be assumed to be apomorphic [**73(1)**]. If the M_{1+2} and M_{3+4} veins comprising the cell m_1 are similar in terms of length, that state may be considered plesiomorphic [**74(0)**], while the case in which the vein M_{1+2} is significantly longer is considered apomorphic [**74(1)**]. The lengths of the M_{1+2} and M_{3+4} veins in extinct Liadopsyllidae and Malmopsyllidae are comparable (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010). Comparing the dimensions of the m_1 and cu_1 cells, no species of Liadopsyllidae in which the cells would differ significantly in terms of size may be indicated. This also considers most extant species. The state in which the m_1 and cu_1 cells are comparable in terms of dimensions has been considered as plesiomorphic [**75(0)**] and when their sizes differ significantly, the state is recognized as apomorphic [**75(1)**].

The vein Rs in psyllids may be long and reach the margin of the wing almost at its apex or significantly closer. In all the extinct species of the Cretaceous and Jurassic periods, the vein Rs is long and ends near the apex of the wing (Becker-Migdisova 1985, Shcherbakov 1988, Ouvrard 2010) – such a state has been established to be plesiomorphic [**76(0)**]. The vein Rs ending much closer than at the apex denotes the apomorphic state [**76(1)**].

In his work regarding Afrotropical psyllids of the family Triozidae, Hollis (1984) has described the character of branching of the vein M into M_{1+2} and M_{3+4} veins in a point before or behind the line connecting the locations in which the Rs and Cu_{1a} veins reach the margin

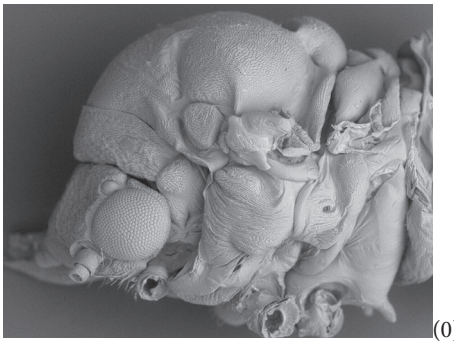
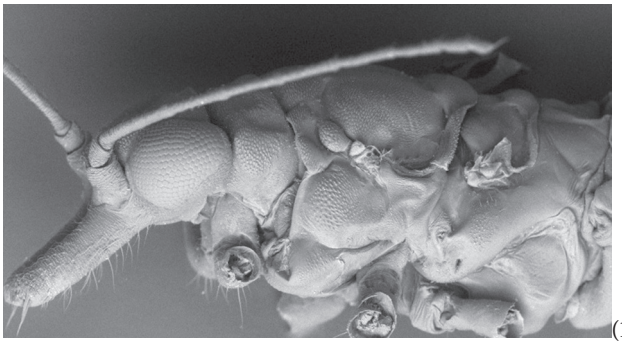
of the wing. This character has not been used in a cladistic analysis to the time, but the branching of the vein M before the line connecting the locations in which the Rs and Cu_{1a} **[77(0)]** veins reach the margin of the wing has been considered as a plesiomorphic state by Hollis (1984). As in all extinct species of the Liadopsyllidae and Malmopsyllidae, the vein M branches before the line connecting the locations in which the Rs and Cu_{1a} veins reach the margin of the wing, and because such a state also dominates in most extant species, it is regarded as plesiomorphic **[77(0)]**, while the branching of the vein M behind the line connecting the locations in which the Rs and the Cu_{1a} veins reach the margin of the wing is considered as an apomorphic state.

The hindwings of psyllids are rarely described and illustrated in publications. This is partially due to the fact that no diagnostic features have been found in them to time. In his cladistic analysis of the species of the Ciriacremini tribe, Hollis (1976) used the distribution of bristles at the anterior costal margin of the hindwings. The uniform distribution of the costal setae was regarded as a plesiomorphic state **[78(0)]**, while grouped costal setae with spaces between the groups were classified as an apomorphic state **[78(1)]**. The remaining two characters of the hindwings that were used in cladistic analyses so far relate to their venation, or more accurately, the presence or lack of the vein M+Cu and the branching of the vein Cu or the lack thereof. The first of the characters, relating to the vein M+Cu, was used by Burckhardt and Basset (2000), who determined that its presence was a plesiomorphic state **[79(0)]** and the lack thereof was apomorphic **[79(1)]**. The second of the characters was used by Hollis and Broomfield (1989), who have determined that the presence of the branched vein Cu was the plesiomorphic state **[80(0)]**, while the lack of it was apomorphic **[80(1)]**. In case of the fossil materials, only the descriptions by Ouvrard et al. (2010) provide information on costal setae that are not grouped but uniformly distributed and on a non-branching vein Cu. However, no information regarding the presence of the vein M+Cu or the lack thereof is provided.

Apart from wings, thorax appendages also include the legs, yet in the case of psyllids only the third pair exhibits characters that are useful in analyses. Hollis and Broomfield (1989) used the distribution of spurs at the distal end of the metatibia for their analyses and have established their presence and uniform distribution in the shape of an open crown as a plesiomorphic character while explaining the apomorphic state as the distribution of spurs in groups. They have not, however, analyzed species the tibia of which were devoid of such spurs. Because the extinct Liadopsyllidae are devoid of apical spurs at the metatibia, such a state is considered as plesiomorphic **[81(0)]**, while the formation thereof is recognized as the apomorphic state. Apomorphy is explained as their regular distribution in the shape of an open crown **[81(1)]** and their presence in groups is also considered apomorphic **[81(2)]**. The second character of the posterior legs that was used for analyses by White and Hodkinson (1985) and by Burckhardt and Ouvrard (2006) relates to the spurs at the first element of the tarsus. They have regarded their presence as a plesiomorphic state **[82(0)]** while regarding the lack thereof as apomorphic **[82(1)]**.

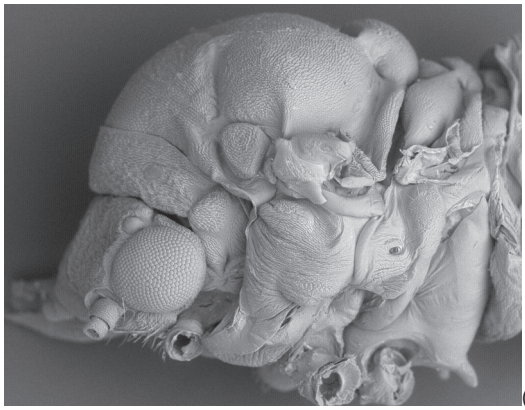
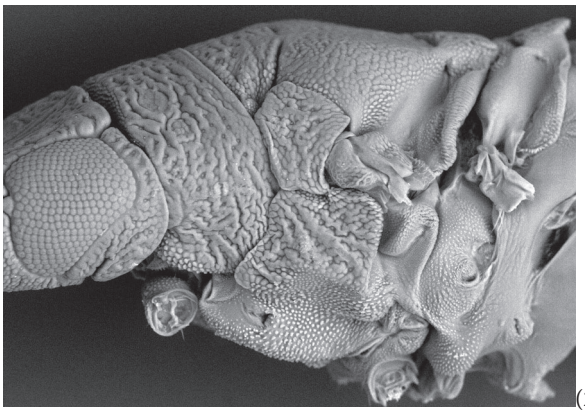
Table 3. List of plesiomorphic and apomorphic characters of psyllids used for preparing the cladogram. „0" indicates plesiomorphic state, digits "1" to "4" indicate a changed state, → indicate the direction of polarisation of character, square bracket includes the work in which the character was used in the cladistic analysis

1. Head strongly inclined in longitudinal body axis 45–90° (0); head weakly inclined in longitudinal body axis 0–45° (1) [Burckhardt 2008].


(0)

(1)

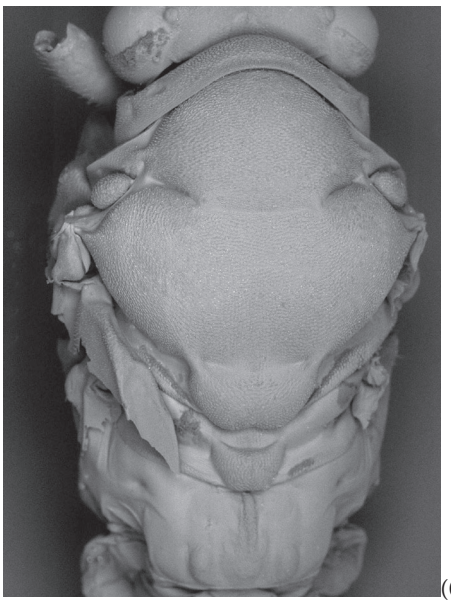
2. In lateral view dorsal margin of thorax weakly arched (0); dorsal margin of thorax strongly arched (1); dorsal margin of thorax almost straight (2).

0→1
↓
2


(0)

(1)

(2)

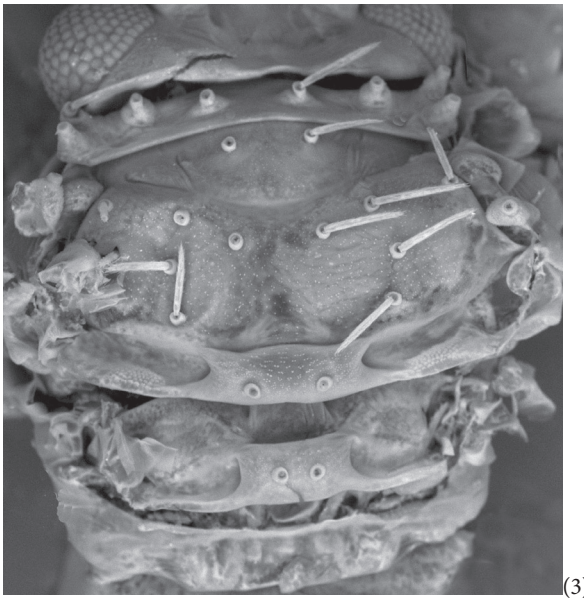
3. Integument of thorax glabrous (0); integument of thorax sparsely delicate setose (1); integument of thorax densely delicate setose (2); integument of thorax sparsely stout-setose (3) [Hollis 1987, modified].

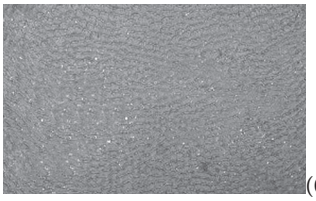
0→1→2
↓
3

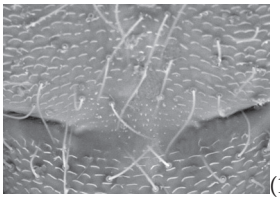

(0)

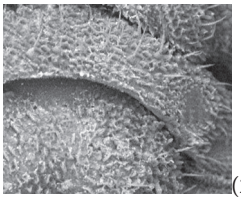

(1)

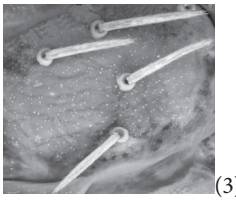

(2)


(3)

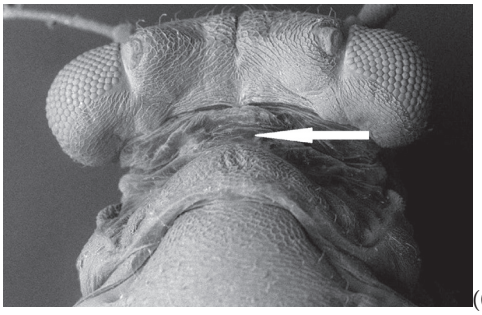

(0)

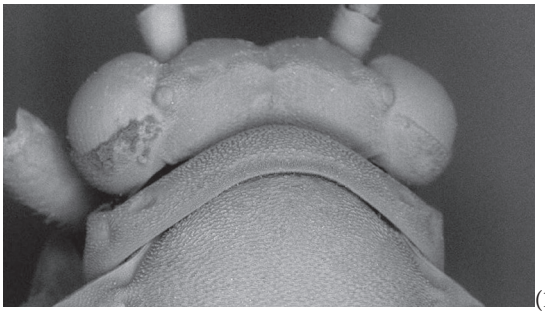

(1)


(2)


(3)

4. Membranous area between head and thorax present (0); absent (1).

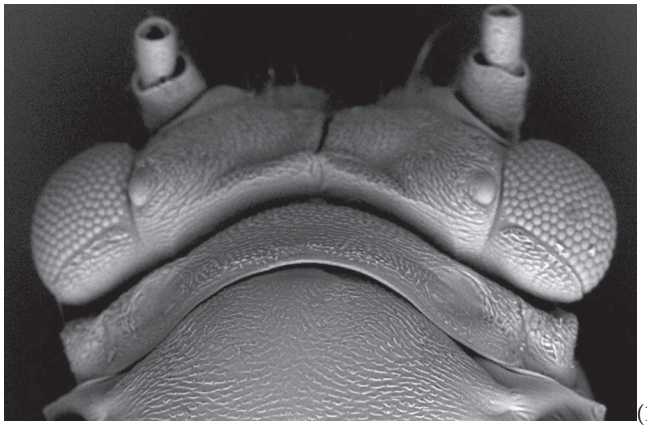

(0)

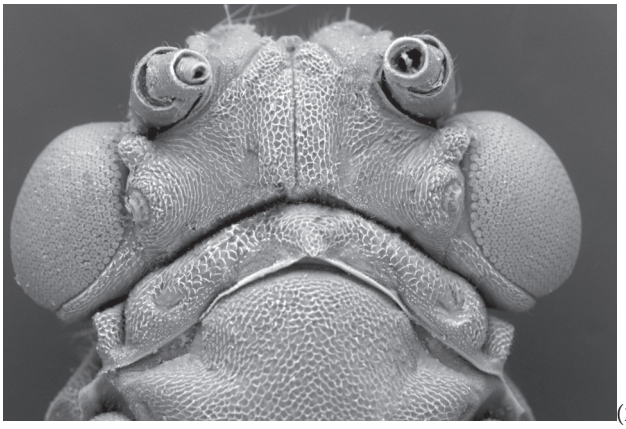

(1)

5. Pronotum as wide as head with compound eyes (0); pronotum slightly narrower than head with compound eyes (1); pronotum distinctly narrower than head with compound eyes (2).

0→1→2

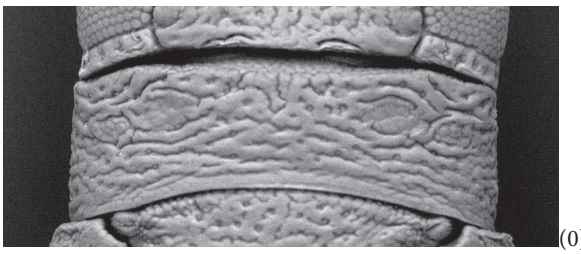

(0)

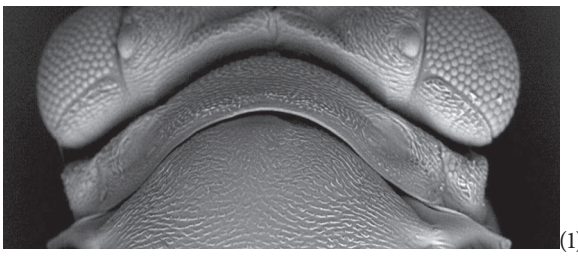

(1)

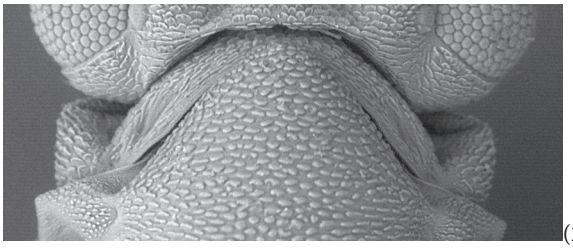

(2)

6. Anterior margin of pronotum almost straight (0); arched (1); u-shaped (2).

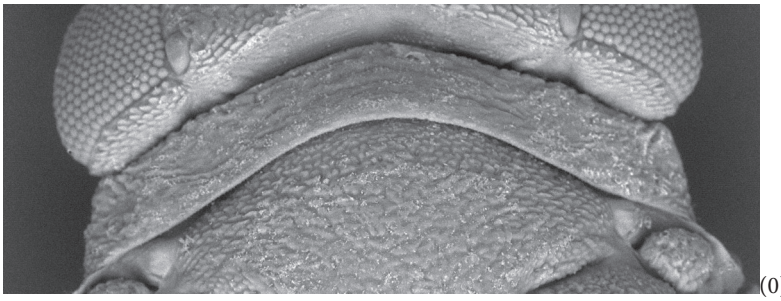
0→1→2

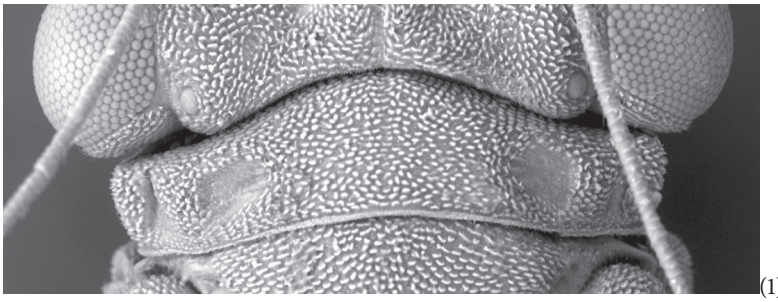

(0)

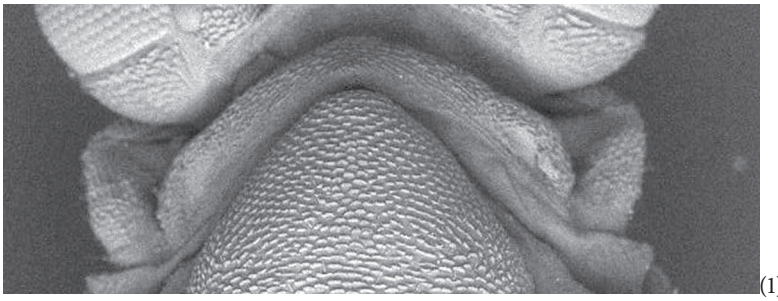

(1)


(2)

7. Pronotum along mid-line as long as along lateral portions (0); pronotum longer or shorter along the mid-line than along lateral portions (1).

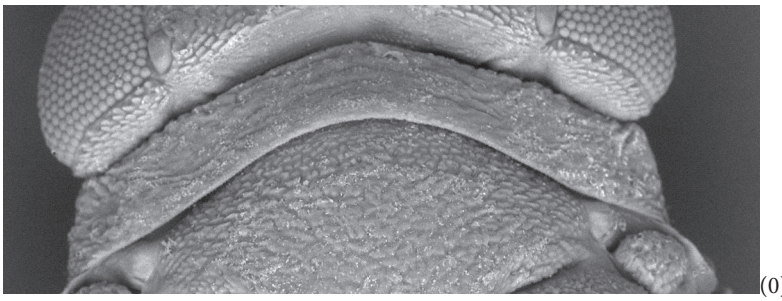

(0)

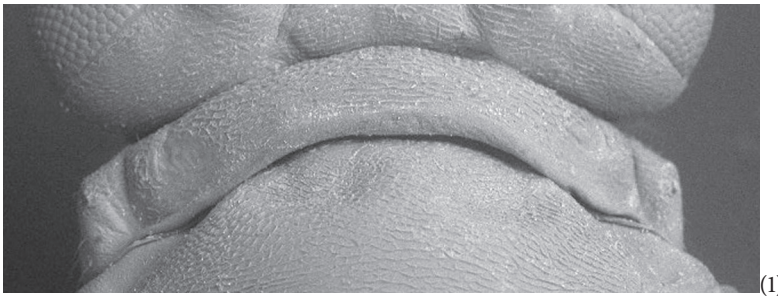

(1)

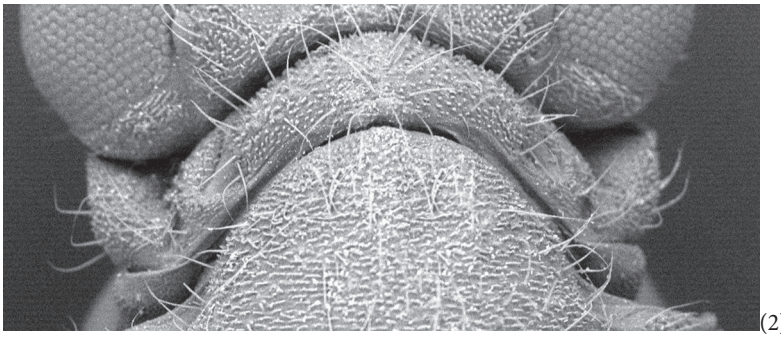

(1)

8. In dorsal view, lateral part of pronotum separated by weak-developed incision, lateral part not protruding anteriad (0); lateral part separated by well-developed incision, lateral part not protruding anteriad (1); lateral part separated by well-developed incision, lateral part protruding anteriad (2).

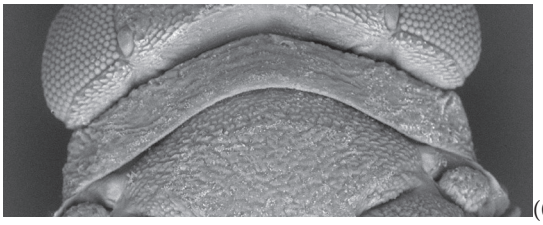
0→1→2

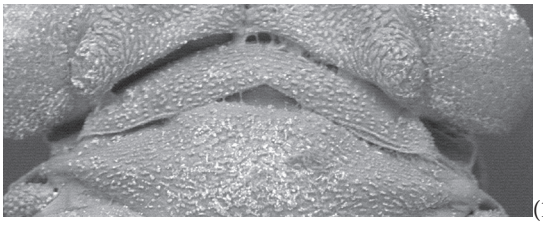

(0)


(1)

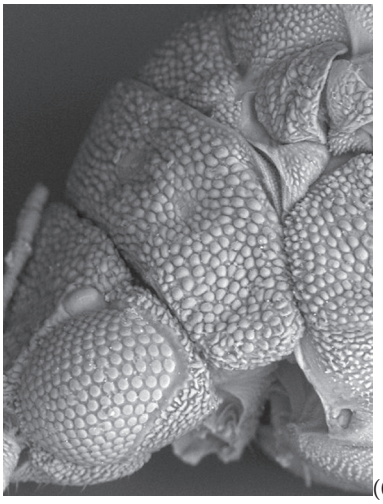

(2)

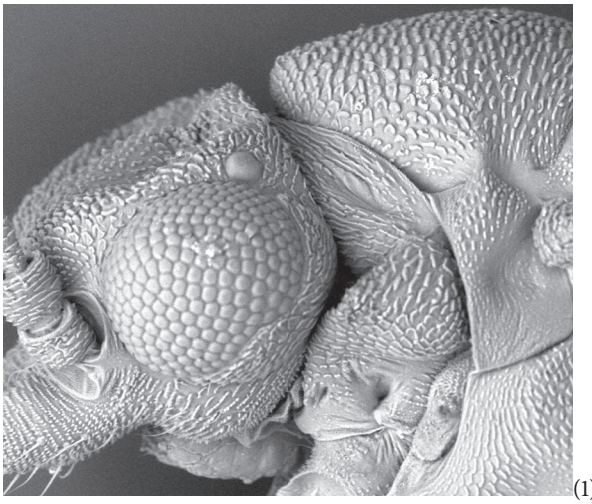
9. Posterior margin of pronotum slightly arched, without incision (0); posterior margin of pronotum slightly arched, with incision (1).


(0)

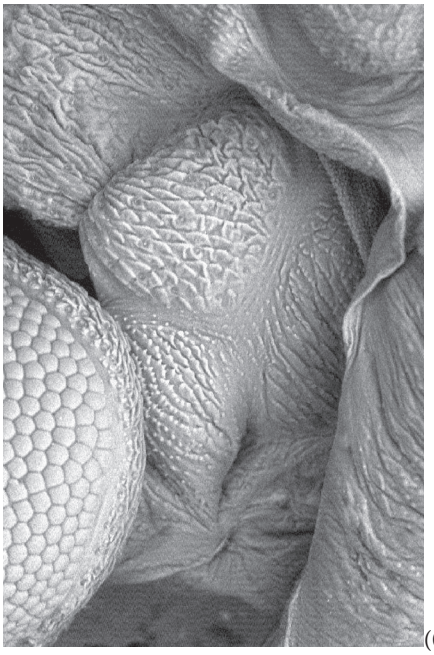

(1)

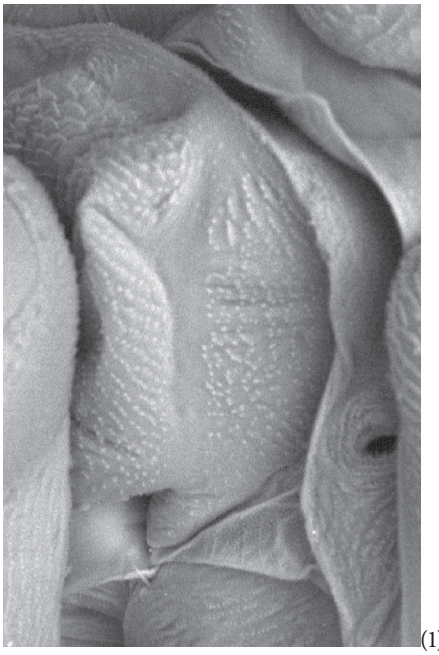
10. Pronotum not vertically or subvertically inclined and not concealed by head (0); pronotum vertically or subvertically inclined and often completely or partly concealed by head (1) [White; Hodkinson 1985, modified].


(0)


(1)

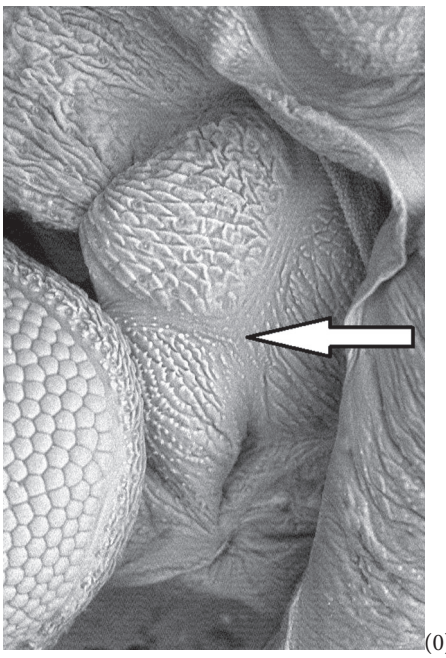
11. Proepisternum and proepimeron the same size (0); proepisternum and proepimeron not subequal (1).

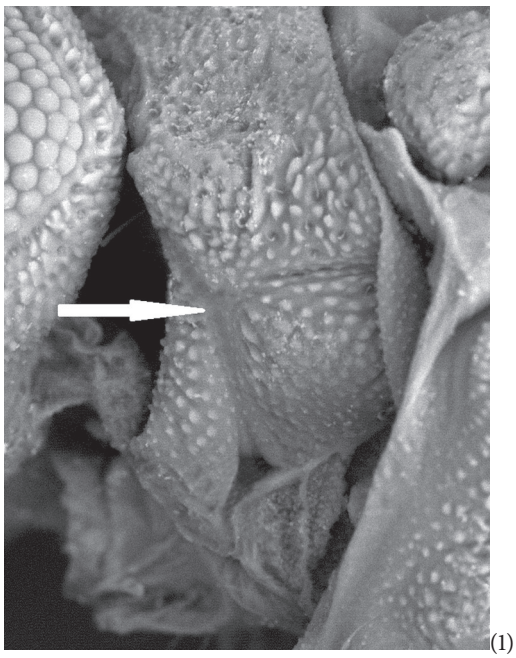

(0)

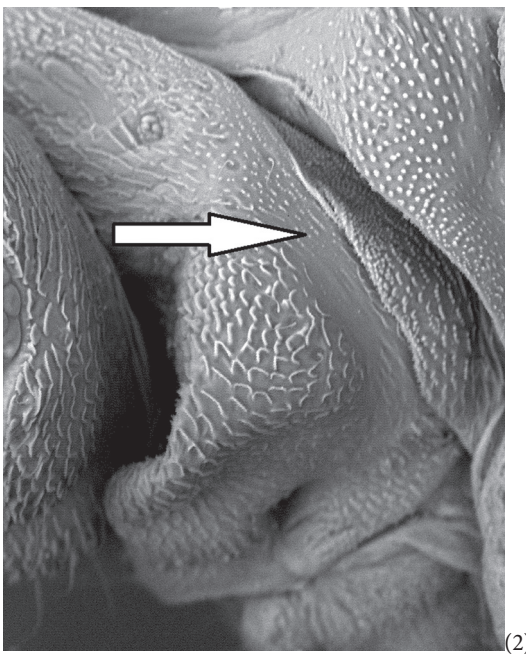

(1)

12. Propleural sulcus dorsally terminating at mid-point of pronotal lateral margin (0); propleural sulcus dorsally terminating at anterior angle of pronotum (1); propleural sulcus dorsally terminating at posterior angle of pronotum (2).

0→1
↓
2

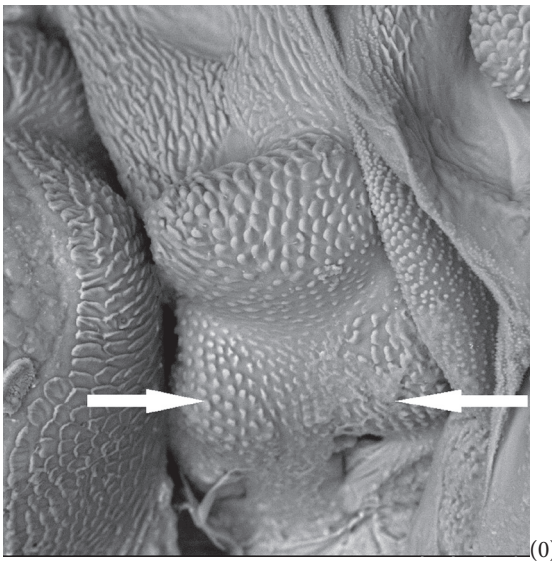

(0)

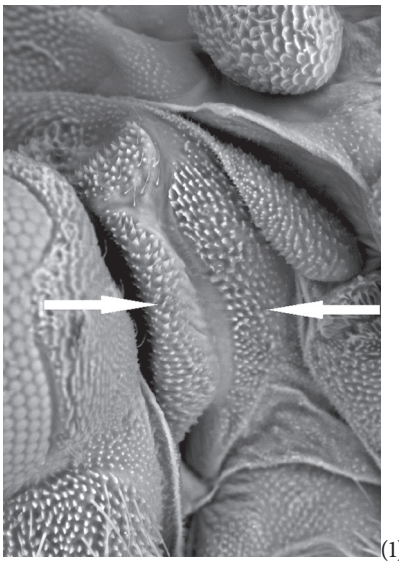

(1)

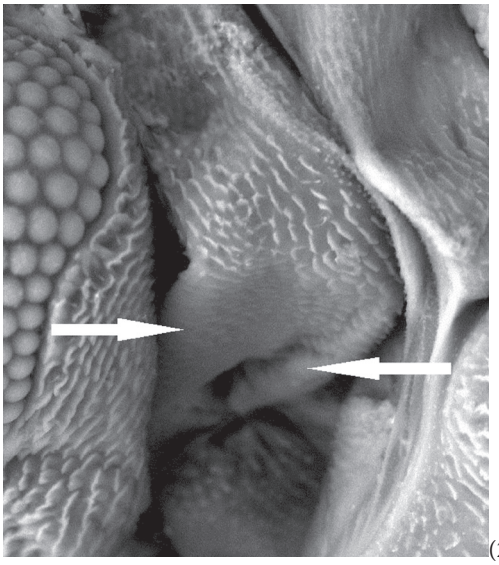

(2)

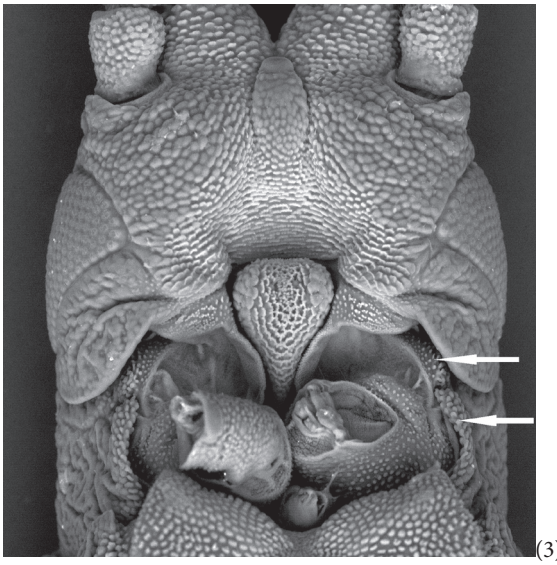
13. Propleurites broad, lateral (0); propleurites narrow, lateral (1); propleurites displaced antero-ventrally (2); propleurites displaced ventrally (3) [Burckhardt, Basset 2000].

0→1→2→3


(0)

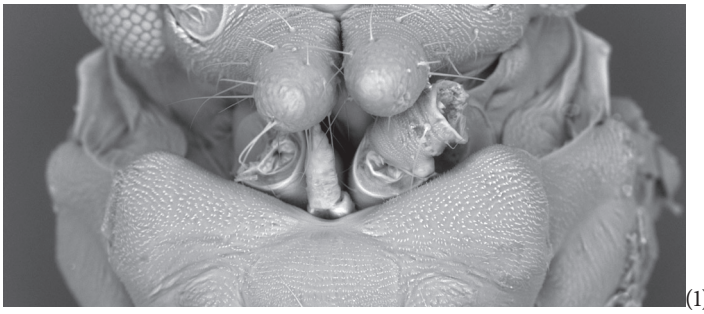

(1)


(2)


(3)

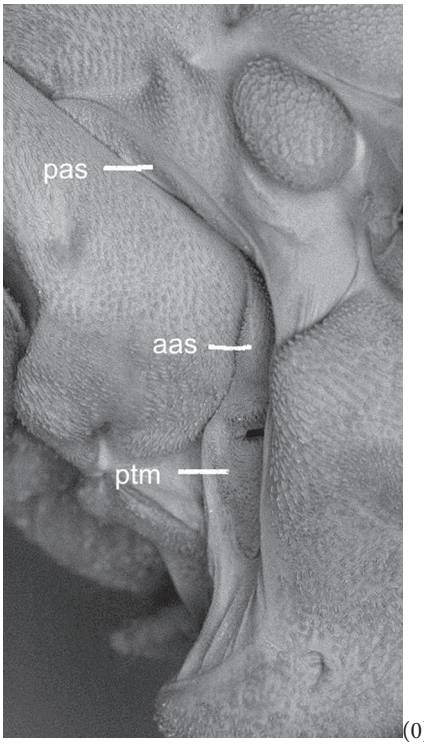
14. Prosternum visible, not covered by fore legs and rostrum (0); prosternum not visible, covered by fore legs and rostrum (1).


(0)

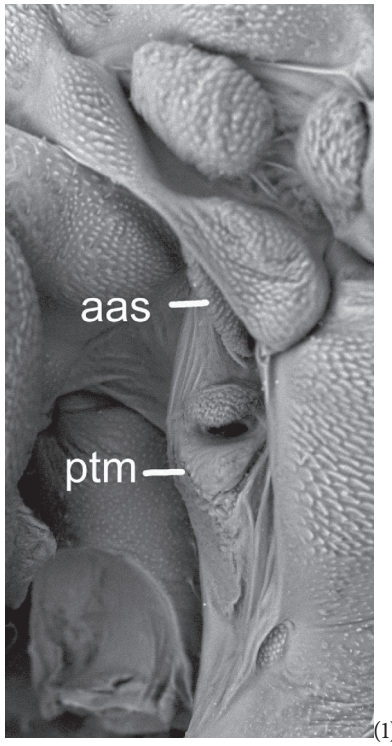

(1)

15. Three additional sclerites between prothorax and mesothorax visible (0); two additional sclerites visible (1); one additional sclerite visible (2).

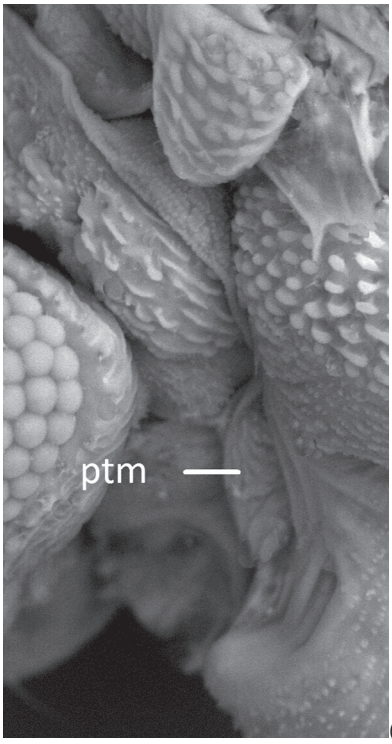
0→1→2



(0)



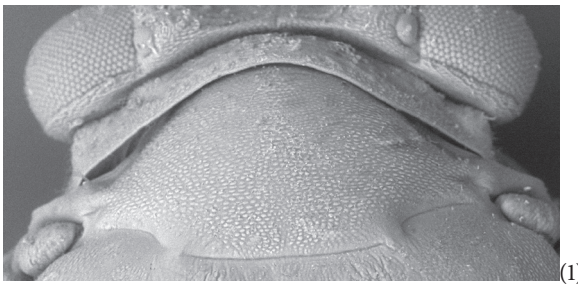
(1)



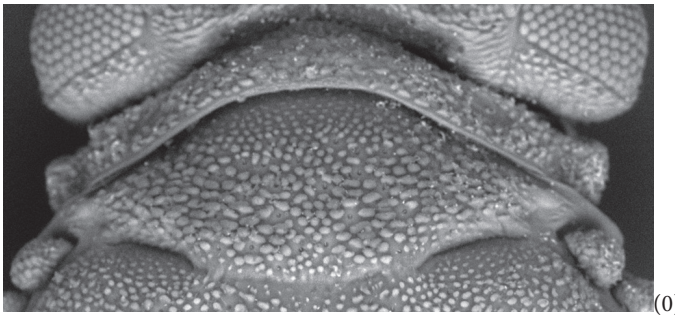
(2)

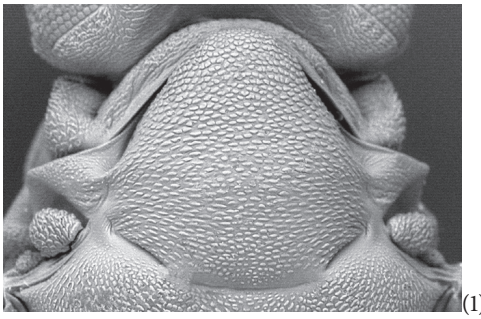
16. Mesopraescutum narrower than pronotum (0); mesopraescutum as wide as pronotum (1).


(0)

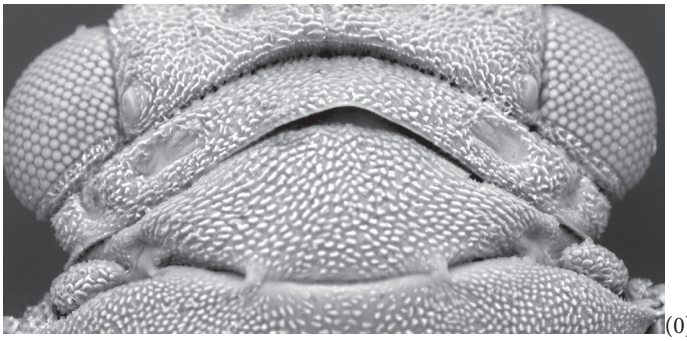

(1)

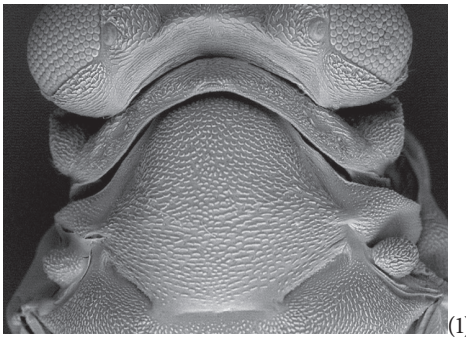
17. In dorsal view mesopraescutum is broader than long (0); mesopraescutum is narrower than long (1).


(0)

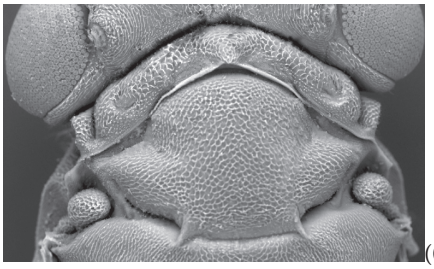

(1)

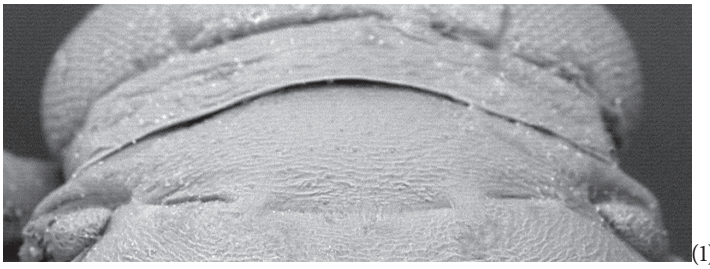
18. Mesopraescutum along less than 3 times as long as pronotum (0); mesopraescutum more than 3 times longer than pronotum along mid-line (1).


(0)


(1)

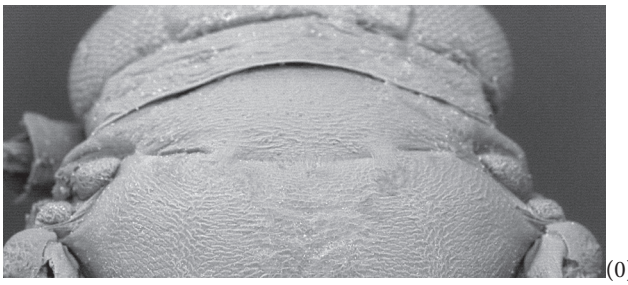
19. Mesopraescutum distinctly separated from mesoscutum (0); mesopraescutum indistinctly separated from mesoscutum (1).

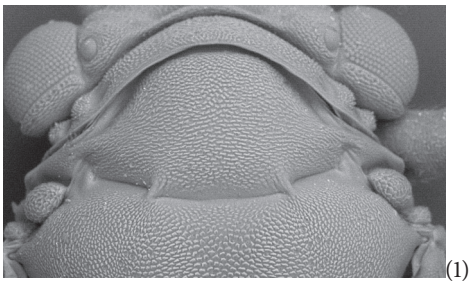

(0)

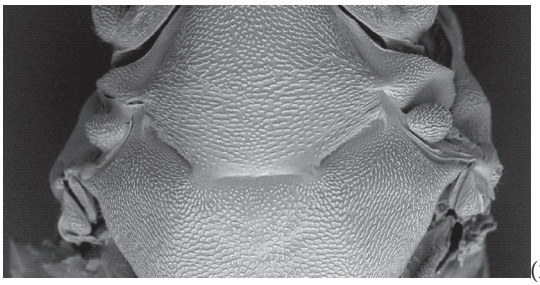

(1)

20. Anterior margin of mesoscutum straight (0); anterior margin of mesoscutum arched (1); anterior margin of mesoscutum u-shaped (2).

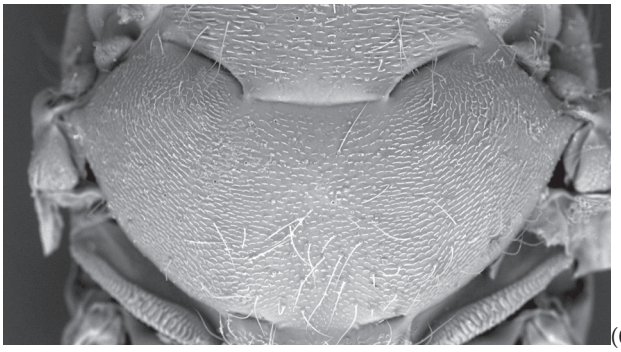
0→1→2


(0)


(1)


(2)

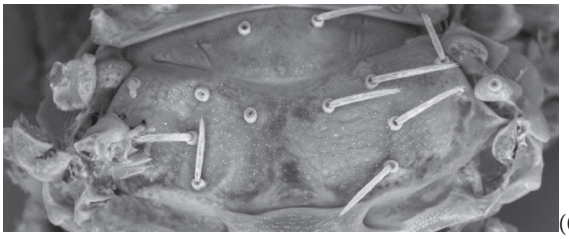
21. In dorsal view mesoscutum is over 2 times broader than long (0); mesoscutum less than twice as broader than long (1).

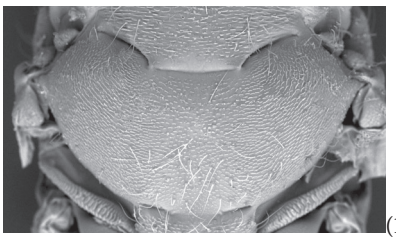

(0)


(1)

22. Ratio F/G (Fig. 4) on mesoscutum is 1 (0); ratio F/G on mesoscutum is about 1.5 (1), ratio F/G is 2 (2).

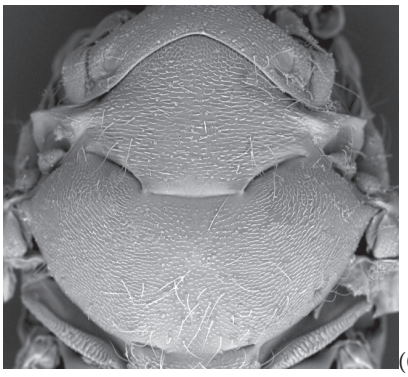
0→1→2


(0)

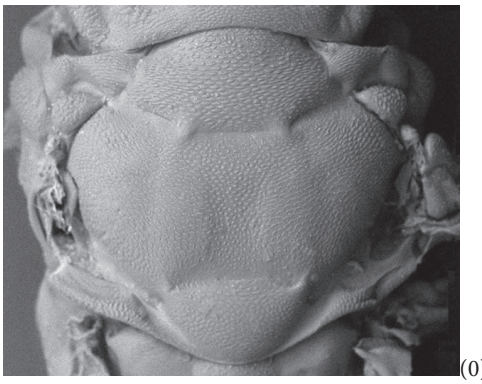
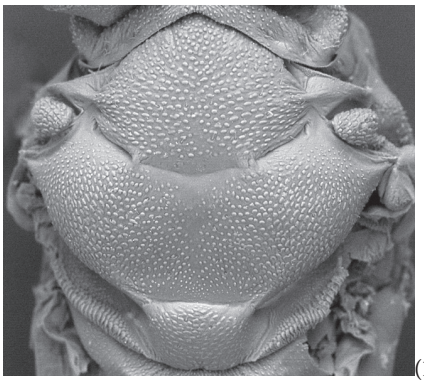

(1)


(2)

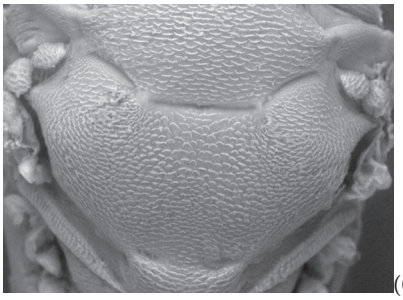
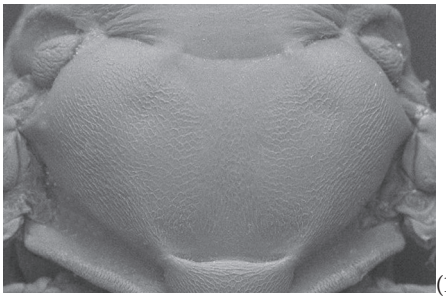
23. Mesoscutum as long as mesopraescutum along mid-line, or slightly longer (0); mesoscutum is 1.5 times longer than mesopraescutum along mid-line (1). Ratio F/D (Fig. 4).

 (0)
 (1)

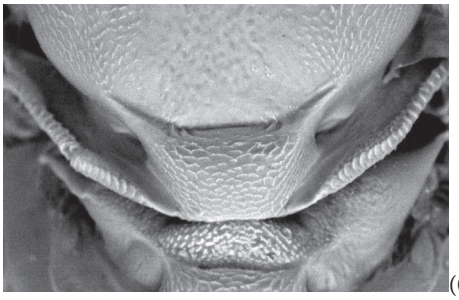
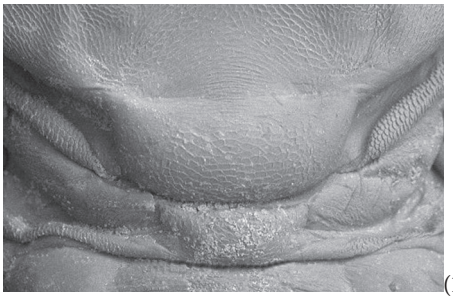
24. Mesoscutum up to 1.5 times as wide as mesopraescutum (0); mesoscutum over 1.5 times broader than mesopraescutum (1).

 (0)
 (1)

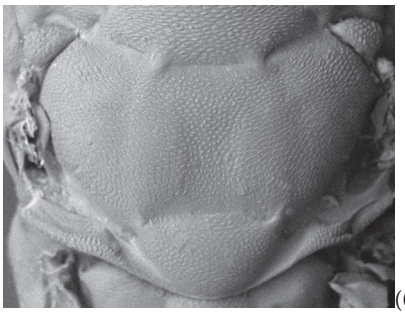
25. Ratio H/G (Fig. 4) of mesoscutum = 1.6–2 (0); ratio H/G = 1–1.3 (1).

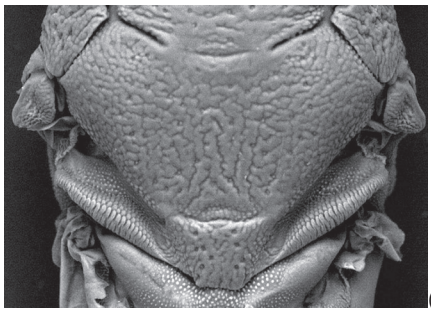
 (0)
 (1)

26. Mesoscutum distinctly separated from mesoscutellum, well visible (0); mesoscutum indistinctly separated from mesoscutellum, hardly visible (1).

 (0)
 (1)

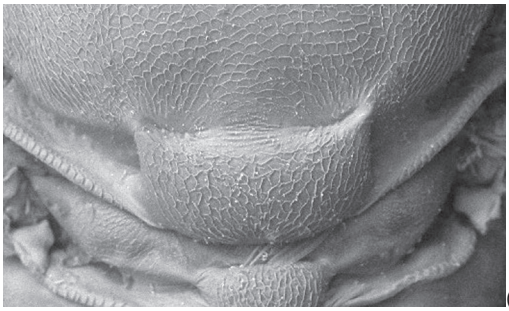
27. Mesoscutellum up to 2.5 times narrower than mesoscutum (0); mesoscutellum over 2.5 times narrower than mesoscutum (1).

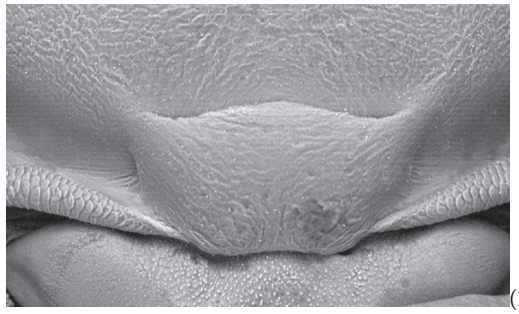

(0)

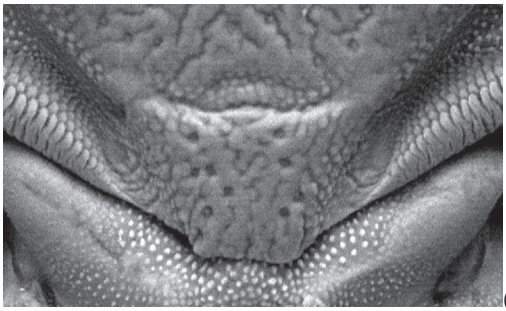

(1)

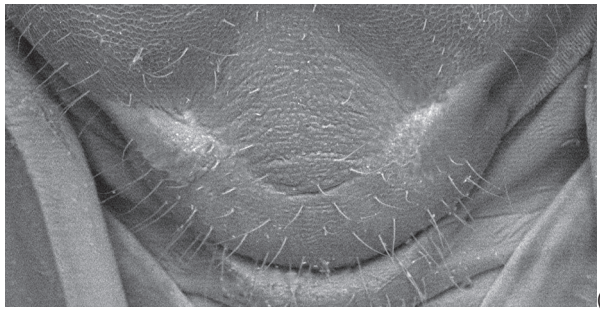
28. Mesoscutellum rectangular (0); mesoscutellum broad, trapezoidal (1); mesoscutellum narrow, trapezoidal (2); mesoscutellum u-shaped (3).

0→1→2
↓
3

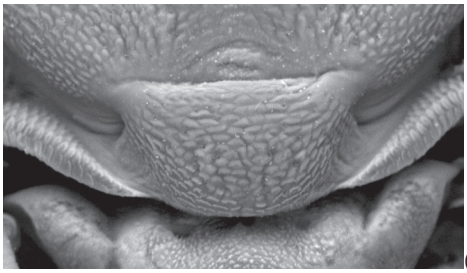

(0)

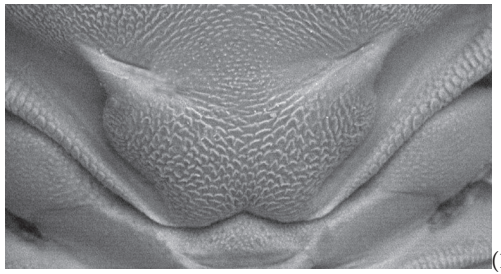

(1)


(2)


(3)

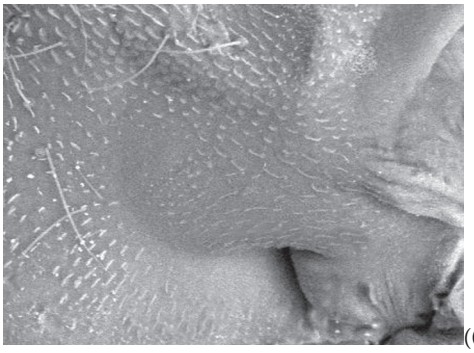
29. Posterior margin of mesoscutellum straight, without incision (0); posterior margin of mesoscutellum with incision in middle (1).

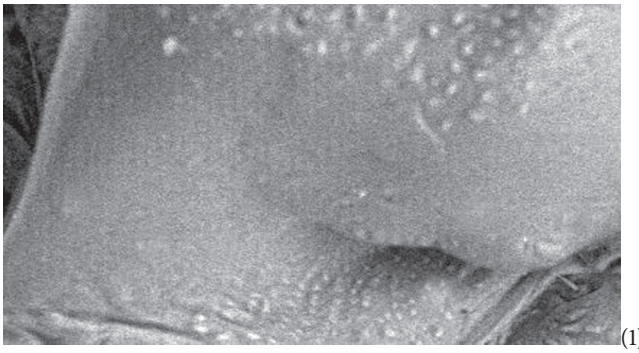

(0)

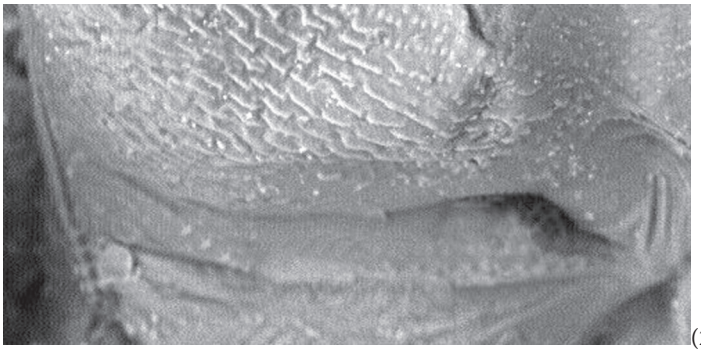

(1)

30. Mesopleural sulcus long, distinct and oblique (0); mesopleural sulcus short (and) or indistinct and oblique (1); mesopleural sulcus almost horizontal (2).

0→1
↓
2

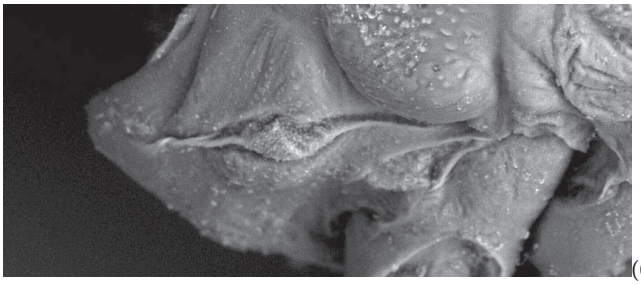

(0)

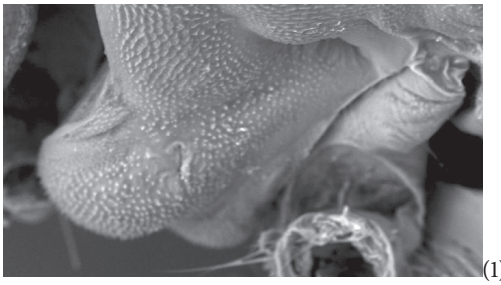

(1)

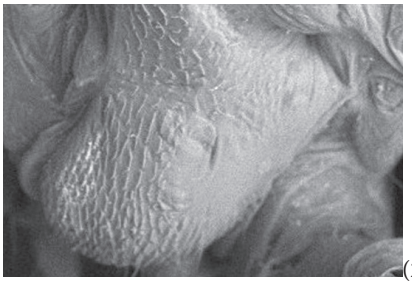

(2)

31. Anapleural cleft (acl2) distinct, almost horizontal and long (0); anapleural cleft distinct, oblique and (or) short (1); anapleural cleft hardly visible (2).

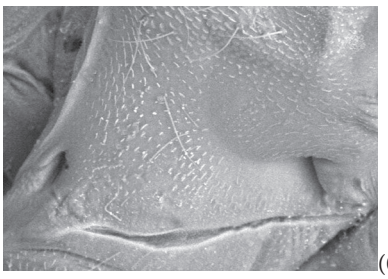
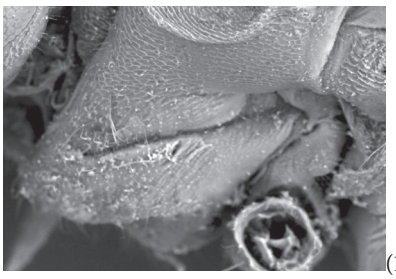
0→1→2


(0)

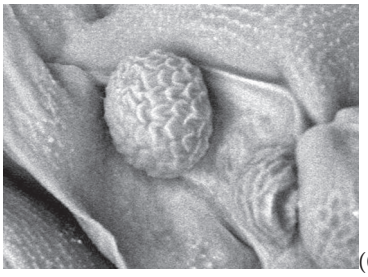

(1)


(2)

32. Pleural sulcus is not connected to anapleural cleft (0); pleural sulcus is connected with anapleural cleft (1).

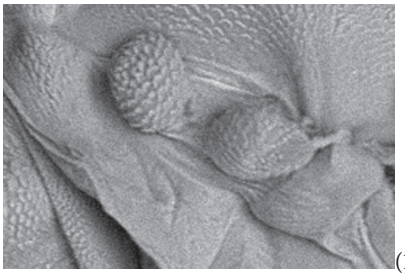

(0)

(1)

33. Parapteron oval (0); parapteron not oval (1).

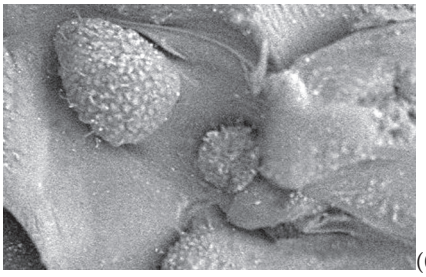

(0)

(1)

34. Parapteron bigger than tegula (0); parapteron and tegula the same size (1).

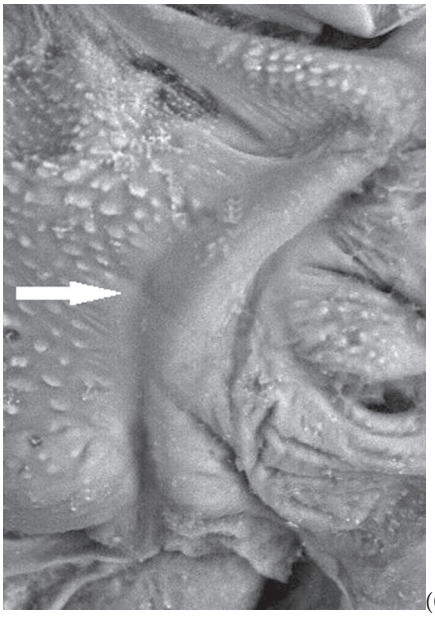

(0)

(1)

35. Tegula oval (0); tegula not oval (1).


(0)

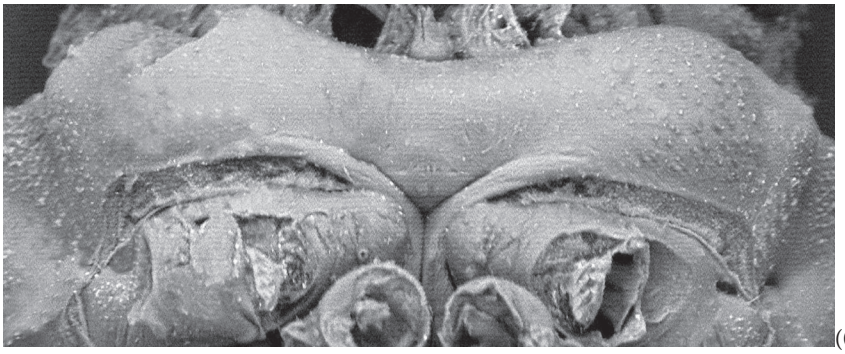
(1)

36. Transepimeral sulcus well-developed (0); transepimeral sulcus hardly visible (1).


(0)

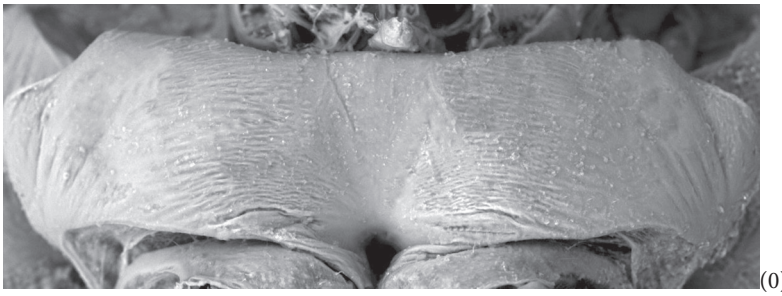

(1)

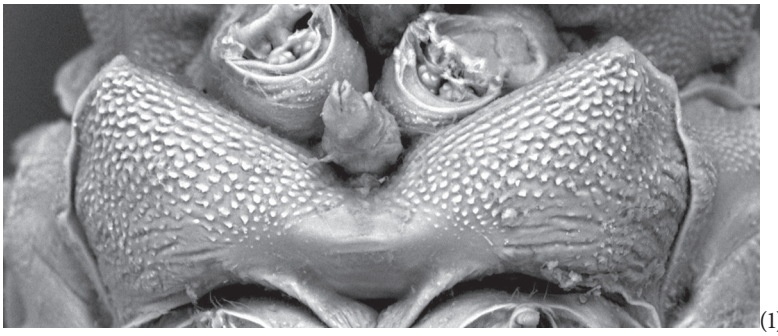
37. In ventral view, tubercle of trochantin anterior of mesocoxa absent (0); tubercle of trochantin anterior of mesocoxa present (1).


(0)

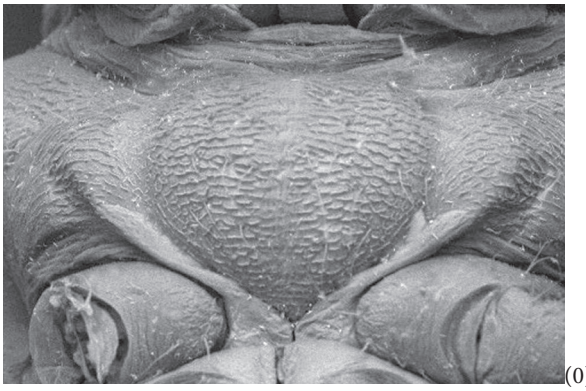

(1)

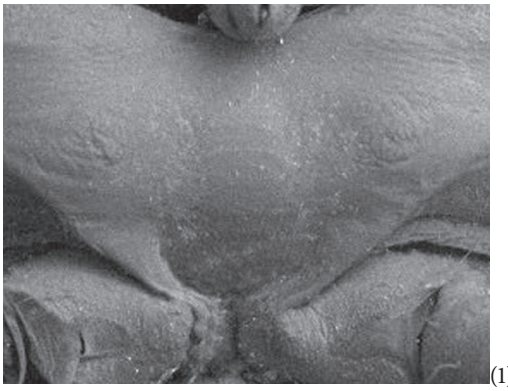
38. Anterior margin of mesosternum straight, without incision (0); anterior margin of mesosternum with incision in the middle (1).

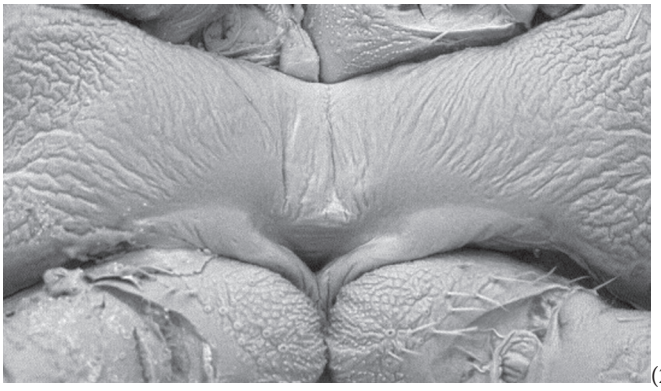

(0)


(1)

39. Pleurosternal suture well visible (0); pleurosternal suture hardly visible (1); pleurosternal suture not visible (2).
0→1→2

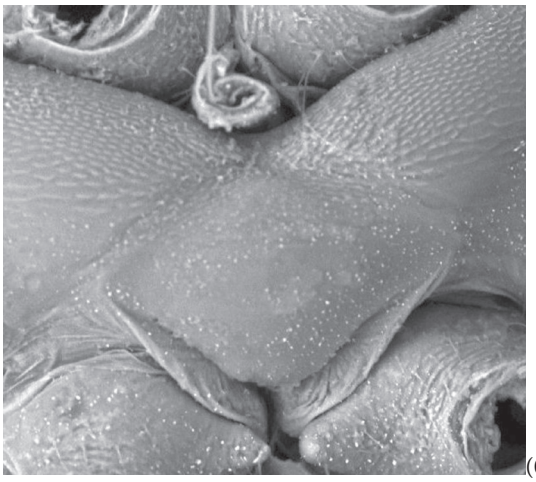

(0)


(1)

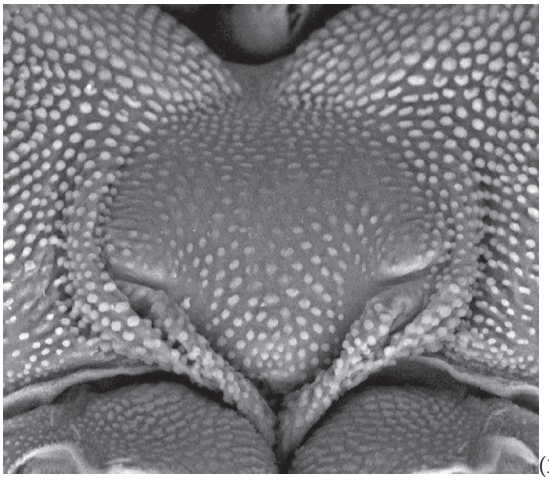

(2)

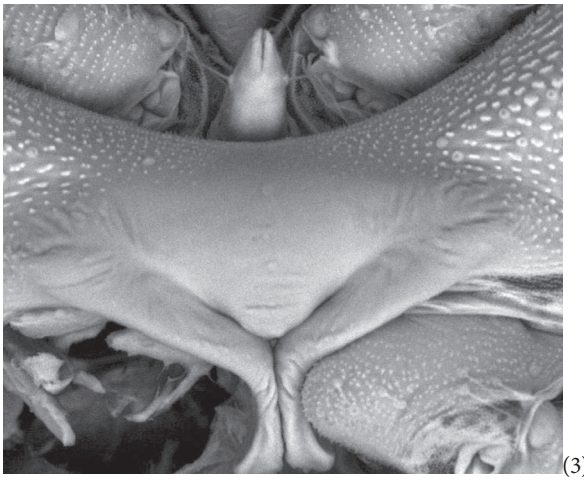
40. Basisternum rhomboidal (0); basisternum oval (1); basisternum mushroom-shaped (2); basisternum triangular (3); shape of basisternum indistinct (4).

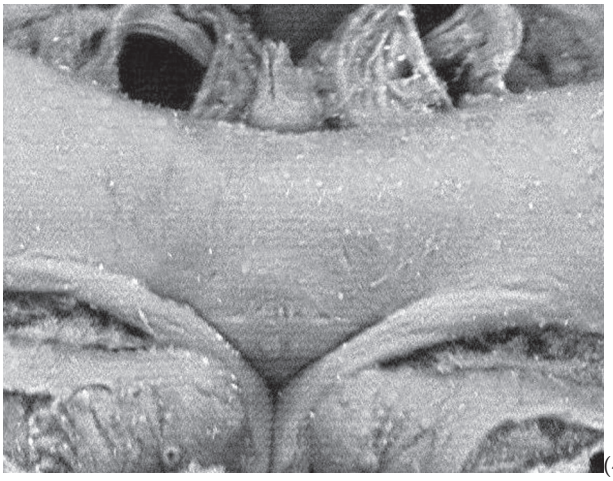
4←0→1→2
↓
3


(0)


(1)

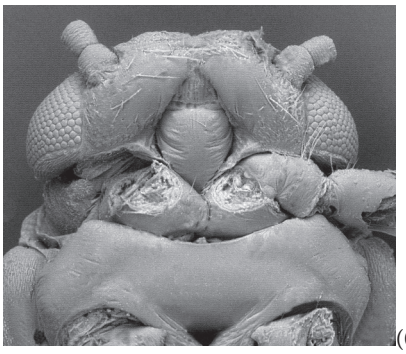

(2)

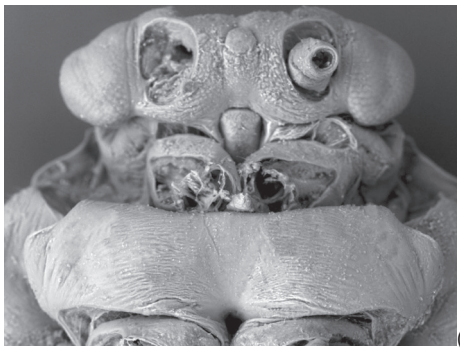

(3)

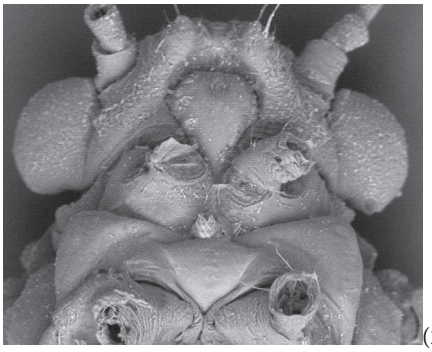

(4)

41. Lateral part of katepisternum in ventral side as wide as width of head with eyes (0); lateral part of katepisternum in ventral side wider than width of head with eyes (1); lateral part of katepisternum in ventral side narrower than width of head with eyes (2).

0→1
↓
2

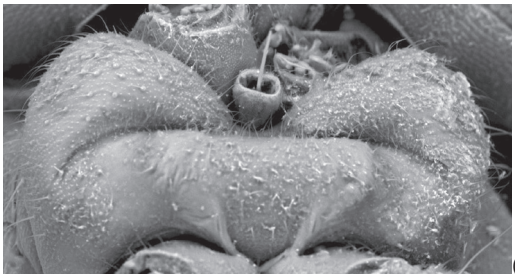

(0)


(1)

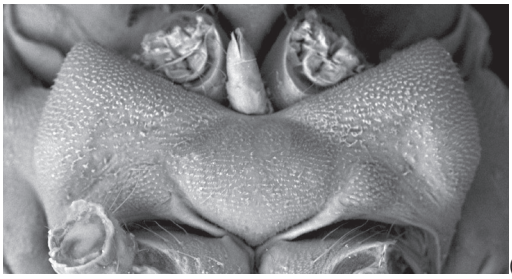

(2)

42. In ventral view anterior protruding of katepisternum is small, oval structure (0); anterior protruding of katepisternum is big, oval structure (1); anterior protruding of katepisternum is structure with a sharp point (2).

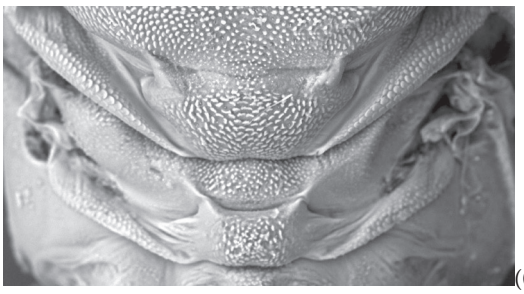
0→1
↓
2

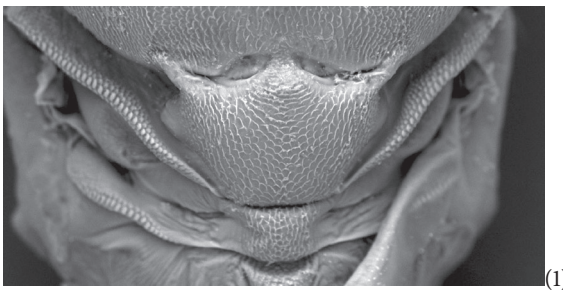

(0)


(1)

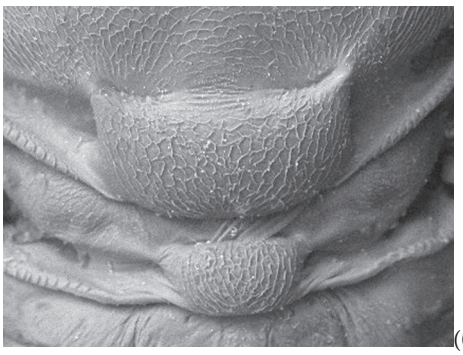

(2)

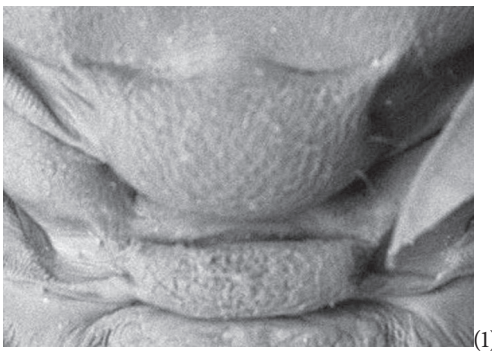
43. Metascutum visible in dorsal view (0); metascutum not visible in dorsal view (1).


(0)

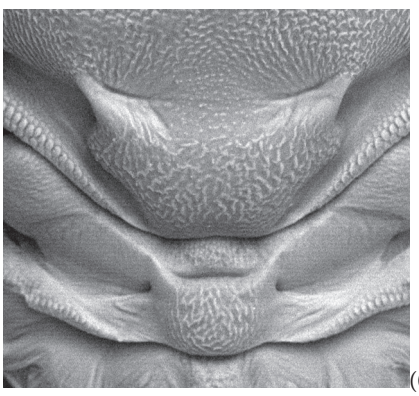

(1)

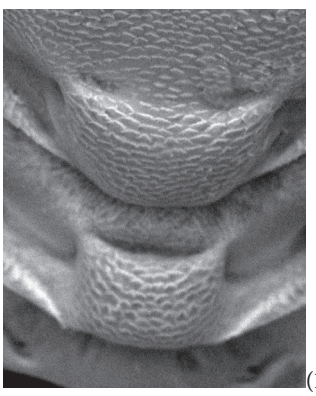
44. Metascutellum about ½ as wide as mesoscutellum (0); metascutellum as wide as mesoscutellum (1). (Ratio M/J, Fig. 4).


(0)

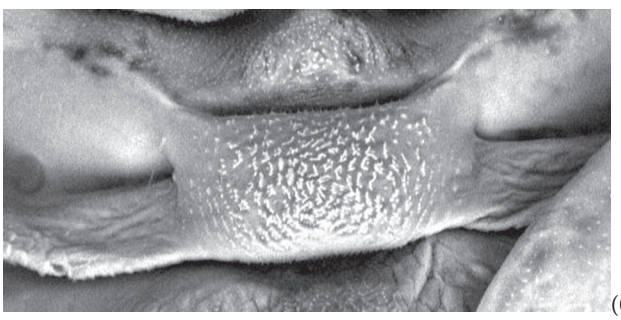

(1)

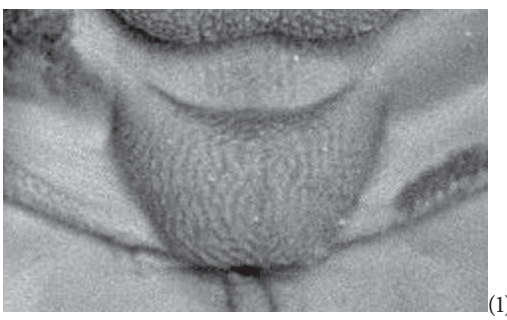
45. Metascutellum shorter than mesoscutellum in mid-line (0); metascutellum as long as mesoscutellum in mid-line (1). (Ratio N/K, Fig. 4).


(0)


(1)

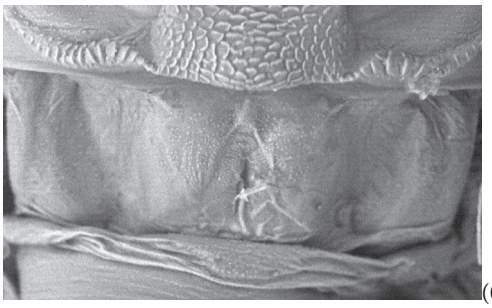
46. Metascutellum rectangular (0); metascutellum trapezoidal (1).

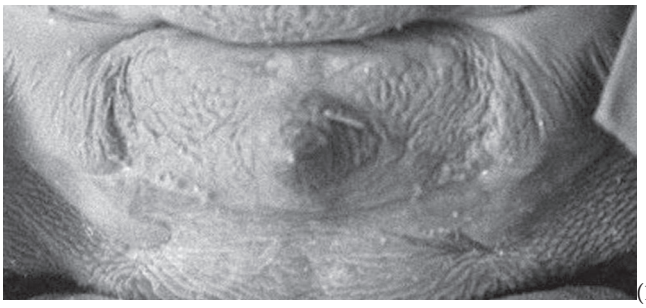

(0)

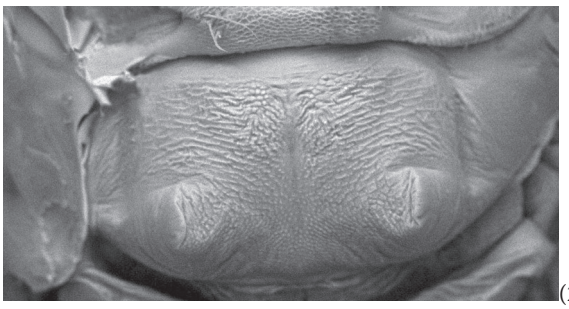

(1)

47. Metapostnotum without any tubercles (0); metapostnotum with one tubercle in the middle (1); pair of tubercles present of metapostnotum (2) [Hollis, Broomfield 1989, modified].

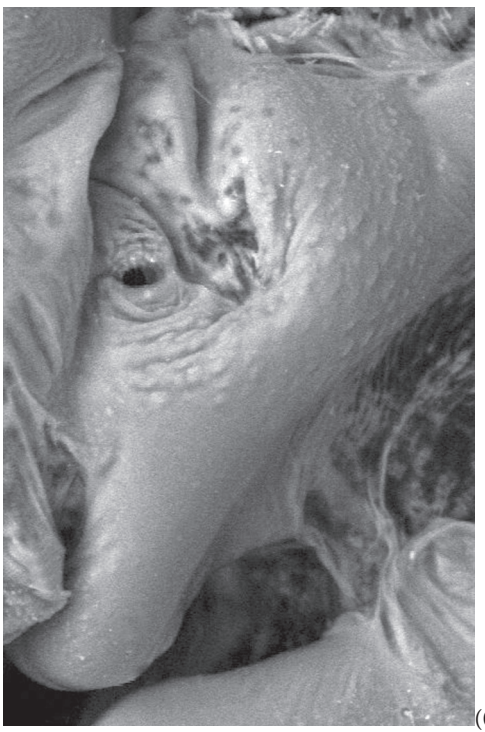
0→1→2

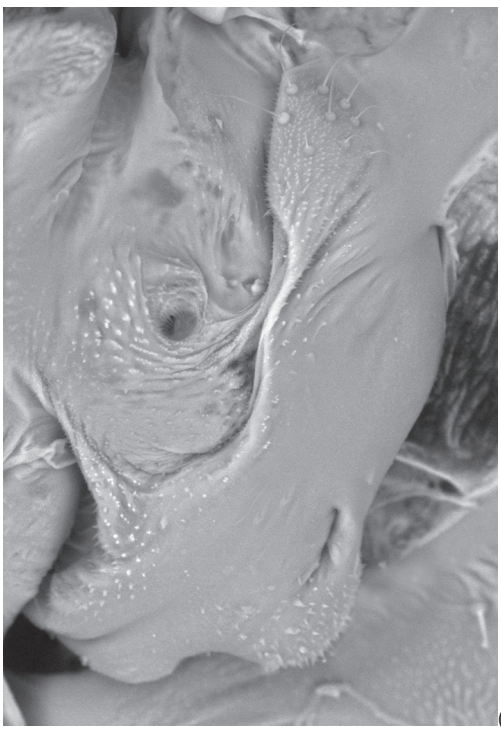

(0)


(1)

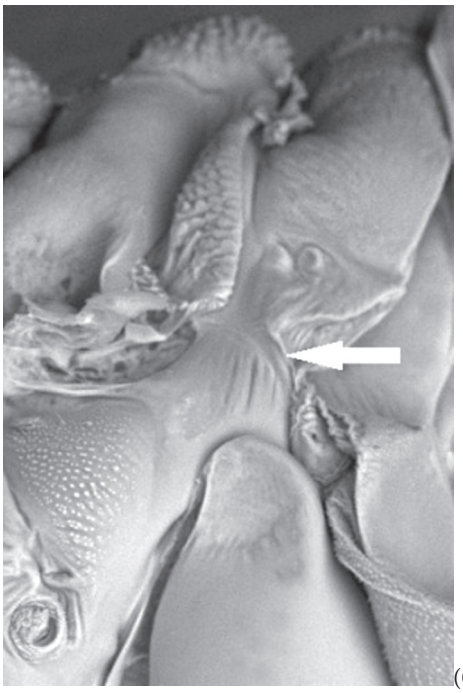

(2)

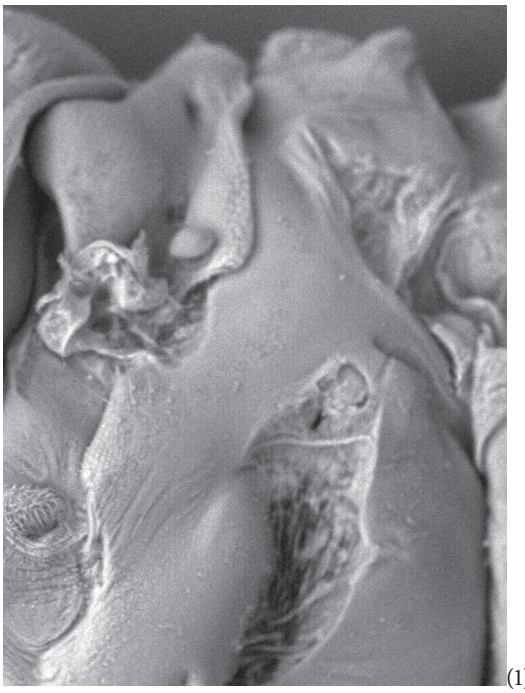
48. Trochantin on metathorax not tuberculated (0); trochantin on metathorax tuberculated (1).


(0)


(1)

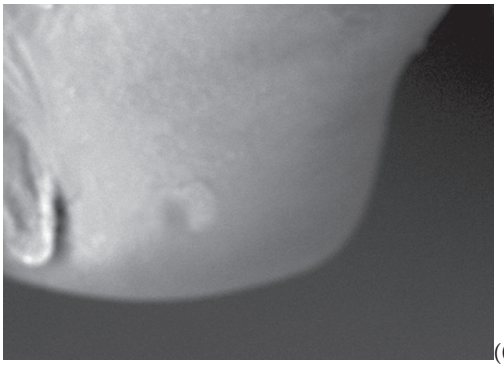
49. Pleural sulcus on metathorax visible (0); pleural sulcus on metathorax not visible (1).

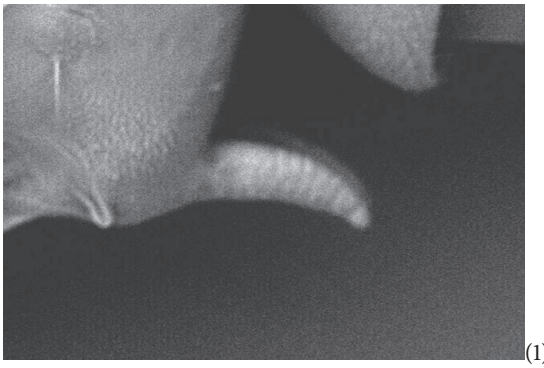

(0)


(1)

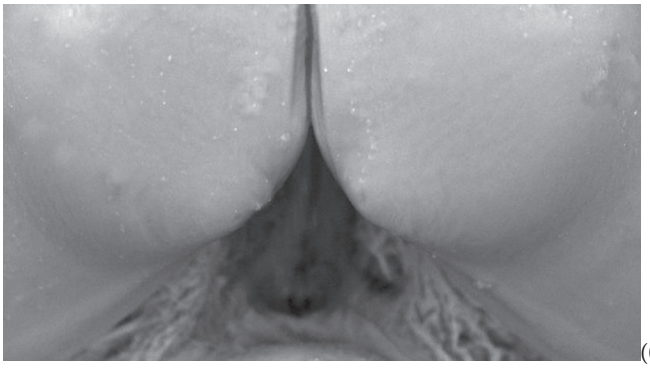
50. Meracanthus absent or very small tubercular (0); meracanthus present horn-shaped (1) [Burckhardt, Lauterer 1989, modified].

Lateral view


(0)


(1)

Ventral view


(0)

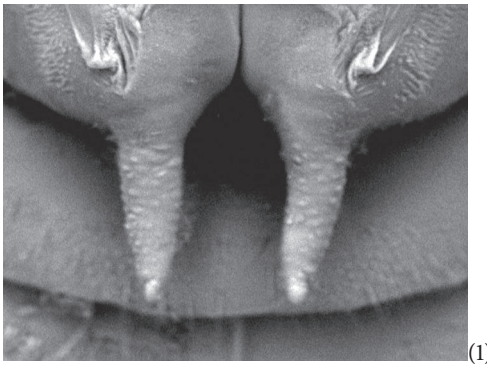
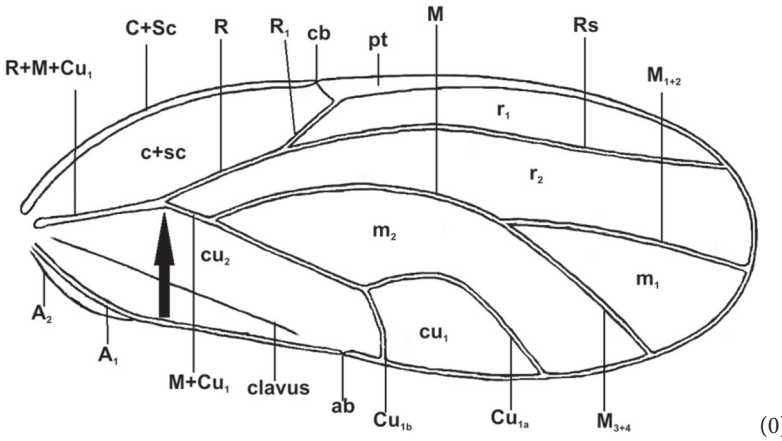
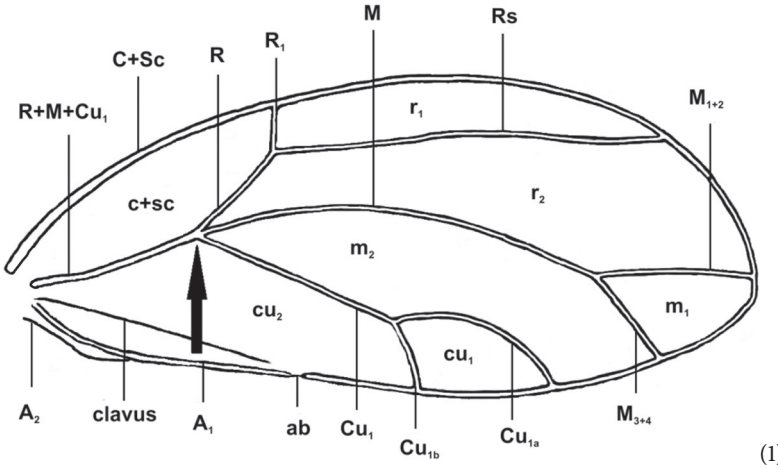

(1)

Table 4. List of plesiomorphic and apomorphic characters of psyllids used for preparing the cladogram encompassing the characters of thorax appendages. ("0" indicates plesiomorphic state; "1" – "2" indicates a changed state; → indicate the direction of polarisation of character; square bracket includes the work in which the character was used in the cladistic analysis)

51. Vein R+M+Cu_1 in forewing bifurcate, giving rise to R and M+Cu_1 (0); vein R+M+Cu_1 trifurcate, giving rise to R, M and Cu_1 (1).

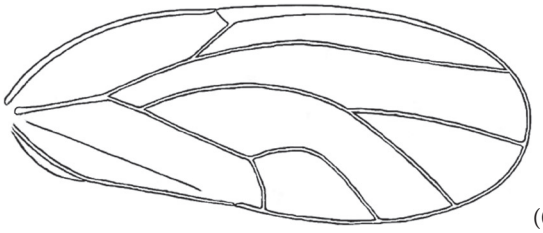


(0)

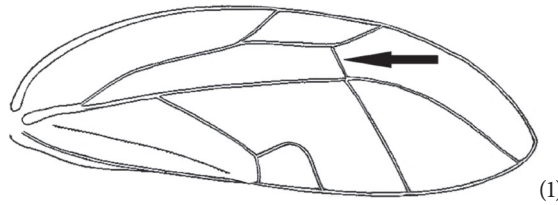


(1)

52. Crossvein between veins Rs and M in forewing absent (0); crossvein between veins Rs and M present (1) [Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt, Ouvrard 2006].

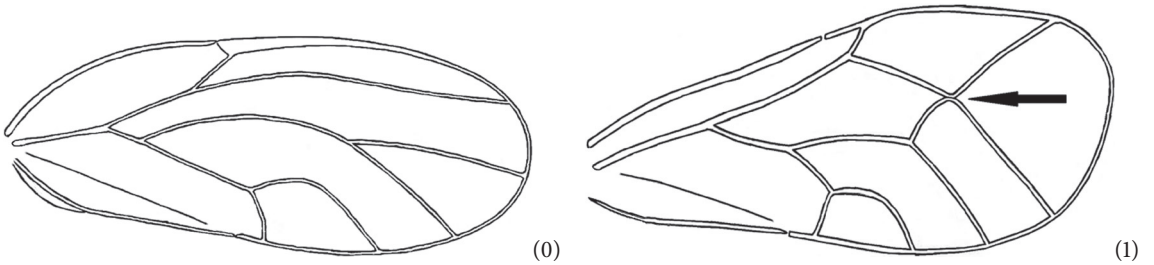


(0)

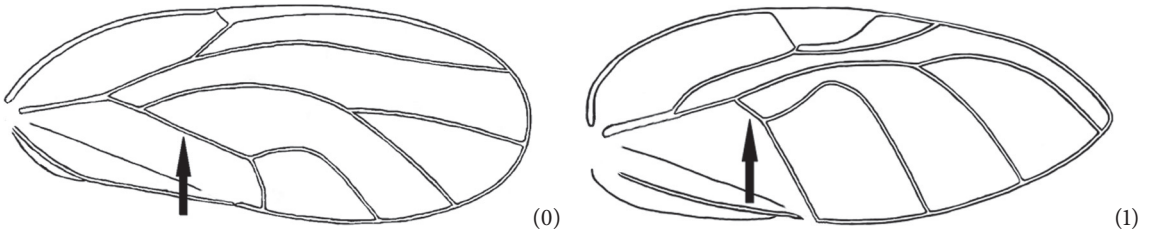


(1)

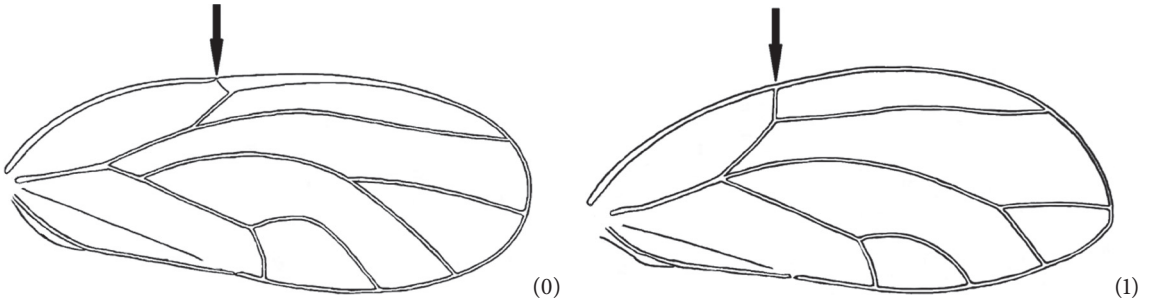
53. Veins Rs and M_{1+2} parallel, not in contact (0); veins Rs and M_{1+2} in contact forming cross (1) [Hollis 1987].



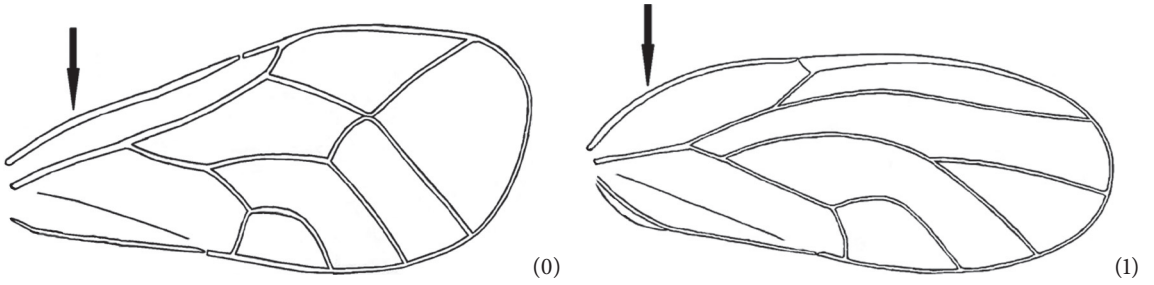
54. Cu_1 stem present, long (0); Cu_1 stem absent or very short (1) [Hollis, Broomfield 1989].



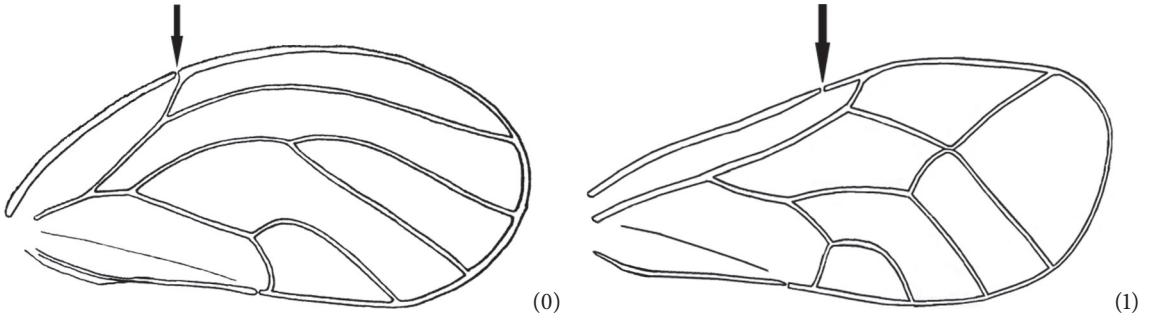
55. Costal break present (0); costal break absent (1) [White, Hodkinson 1985; Hollis 1987; Hollis, Broomfield 1989; Burckhardt, Lauterer 1989; Burckhardt, Basset 2000].



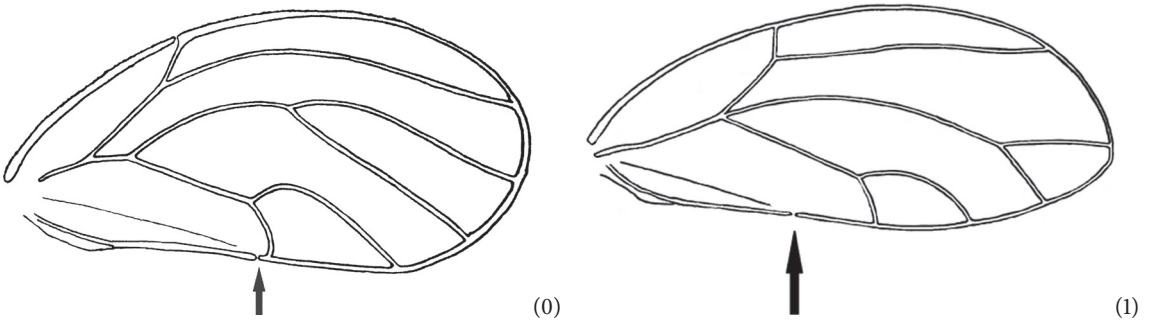
56. Costal margin not curved (0); costal margin curved (1) [White; Hodkinson 1985].



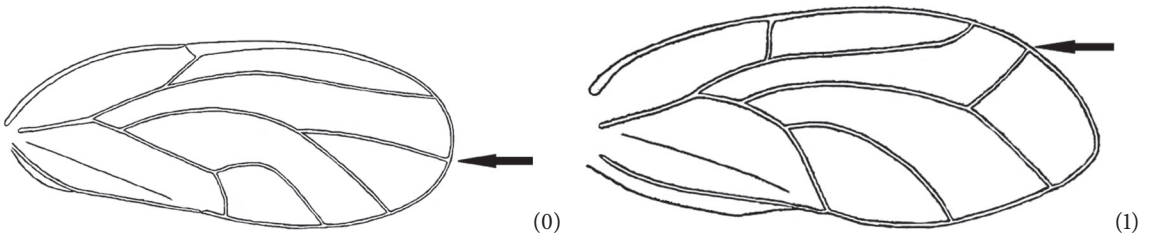
57. Costal break near vein R_1 (0); costal break in distance of vein R_1 (1).



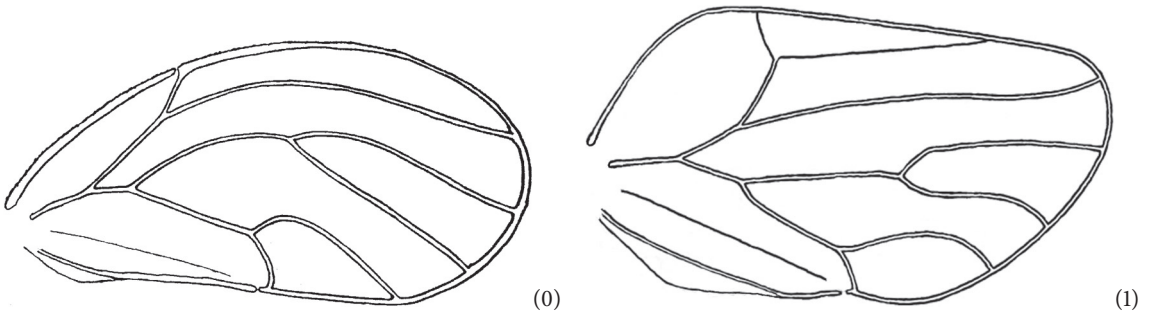
58. Anal break near apex of vein Cu_{1b} (0); anal break in distance of apex of vein Cu_{1b} (1).



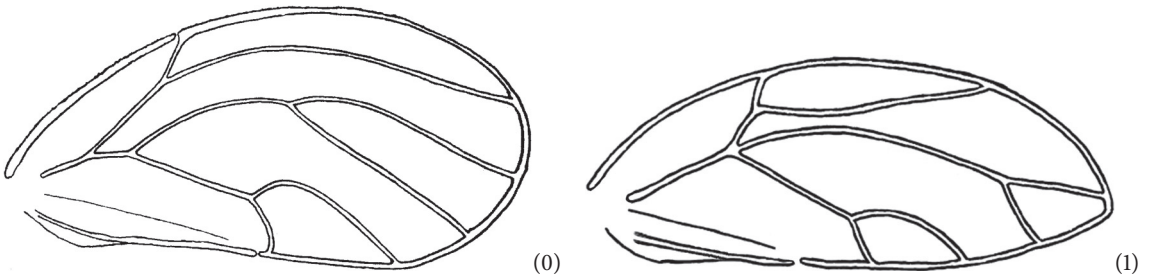
59. Vein M_{1+2} reaching wing margin posteriorly to apex of wing or in apex of wing (0); M_{1+2} reaching wing margin anteriorly to apex of wing (1) [Hollis, Broomfield 1989, modified].



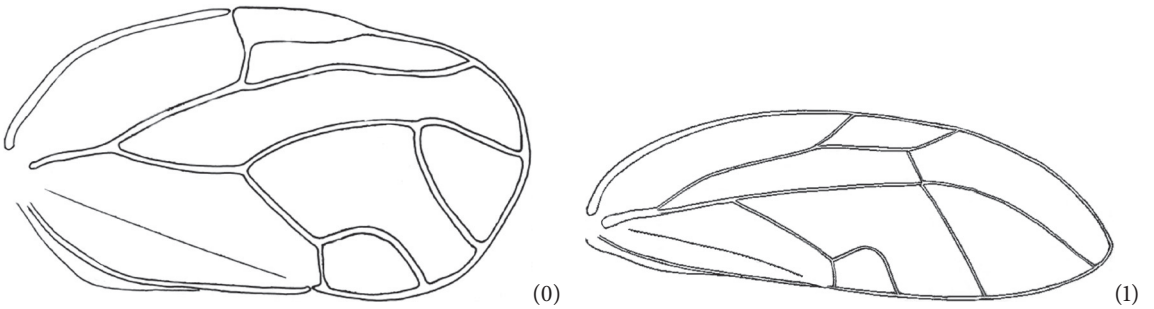
60. Forewing widest in apical third or in the middle (0); forewing widest in basal third (1) [Burckhardt, Ouvrard 2001, modified].



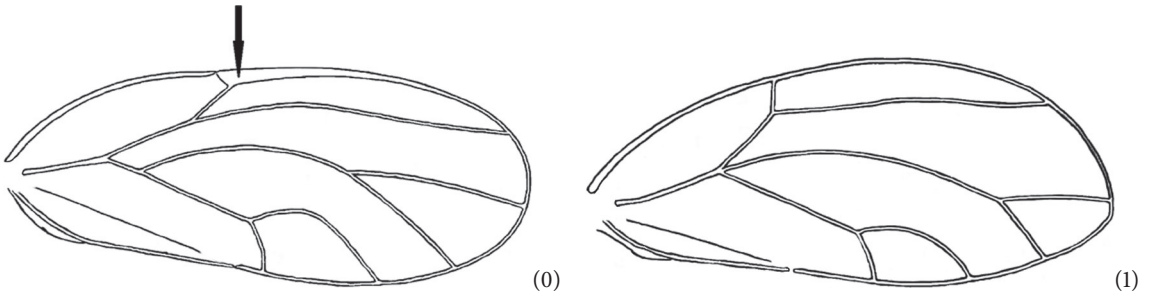
61. Forewing rounded apically (0); forewing angular apically (1) [Hollis 1984, 1987].



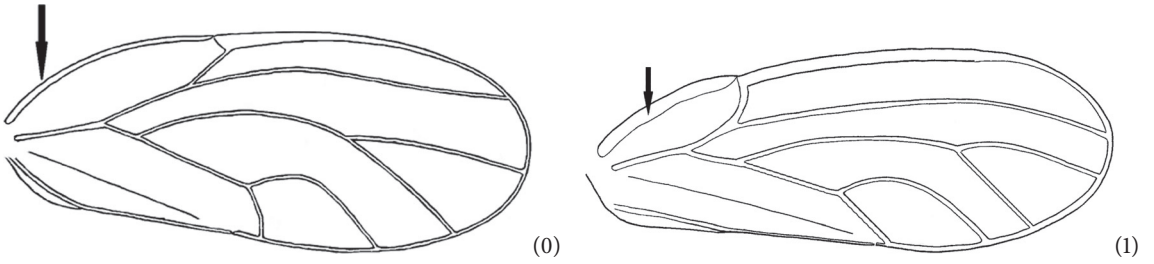
62. Forewing broad (0); forewing narrow (1) [Hollis 1987].



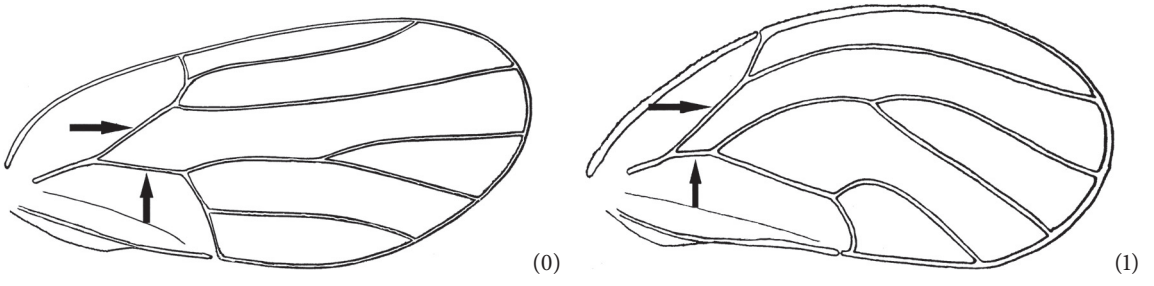
63. Pterostigma present (0); pterostigma absent (1) [White, Hodkinson 1985; Hollis 1987; Burckhardt, Lauterer 1989].



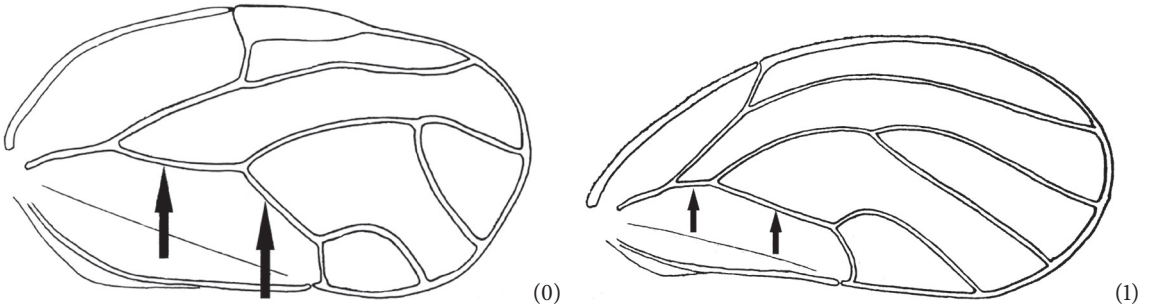
64. Forewings without narrow vein C+Sc (0); forewing with narrow vein C+Sc (1) [Burckhardt, Lauterer 1989].



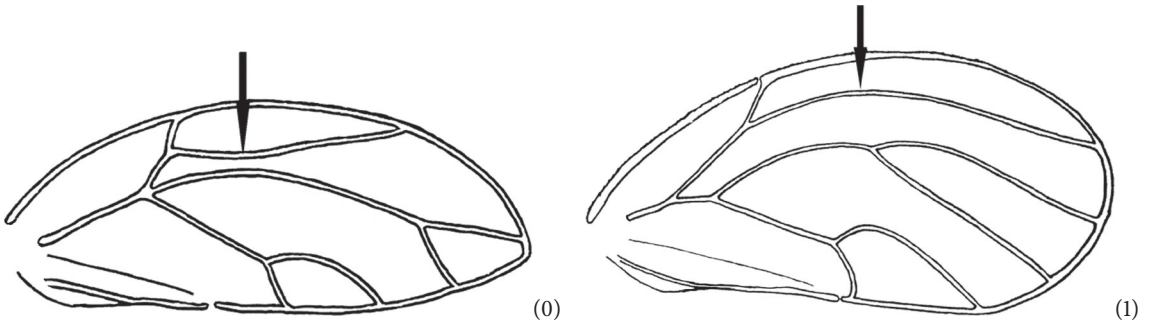
65. Vein R as long as vein M+Cu_1 (0); vein R much longer or shorter than vein M+Cu_1 (1) [Burckhardt 1991, modified].



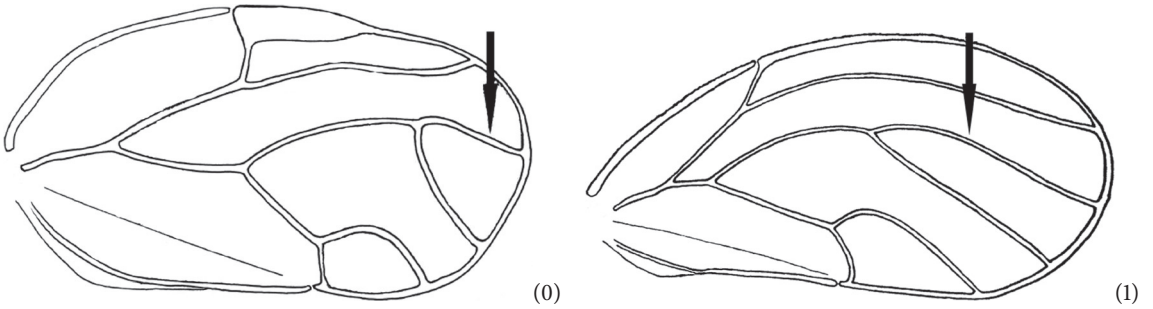
66. Cu stem about as long as M+Cu stem (0); Cu stem longer or shorter than M+Cu stem (1) [Burckhardt 1991, modified].



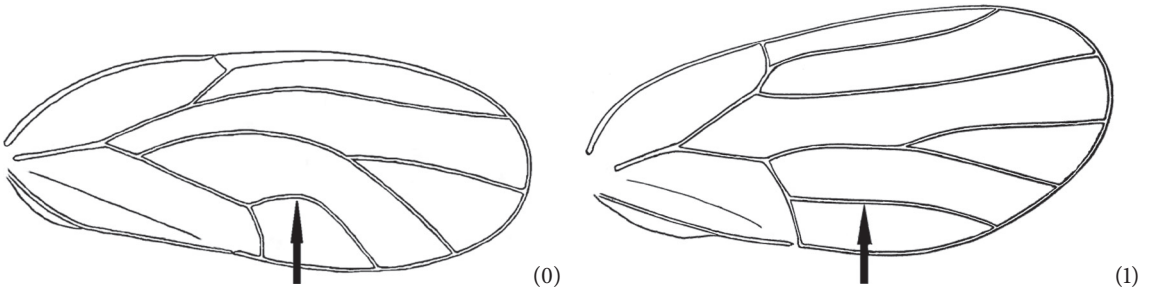
67. Vein Rs straight or curved backwards (0); vein Rs curved forwards (1) [Burckhardt, Basset 2000].



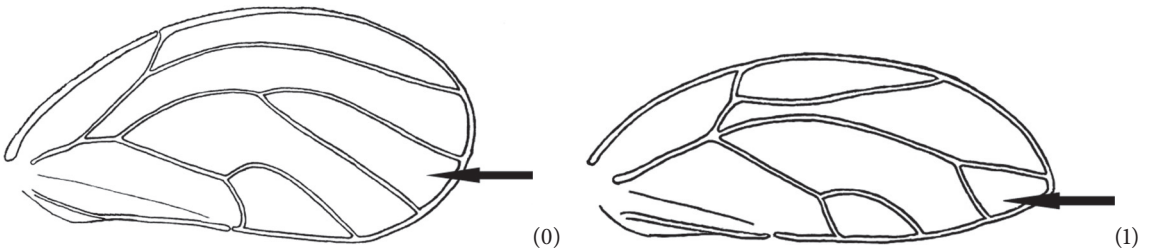
68. Vein M_{1+2} curved backwards (0); vein M_{1+2} curved forwards (1) [Burckhardt, Basset 2000].



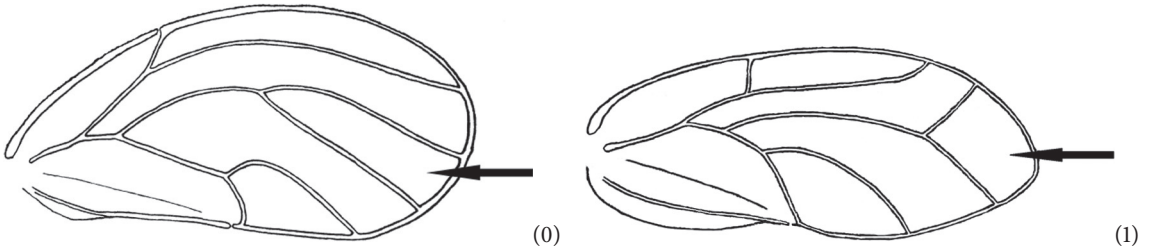
69. Vein Cu_{1a} of forewing moderately convexly curved (0); vein Cu_{1a} weakly convexly curved or almost straight (1) [Burckhardt, Ouvrard 2001, modified].



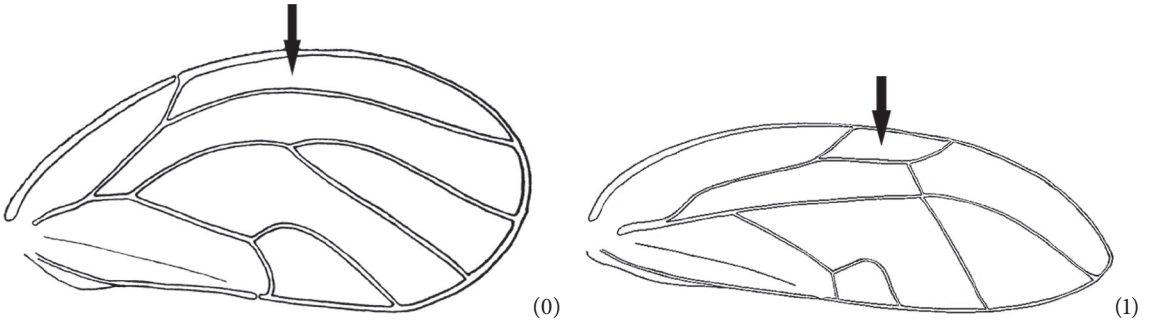
70. Cell m_1 large (0); cell m_1 small (1) [Hollis 1984].



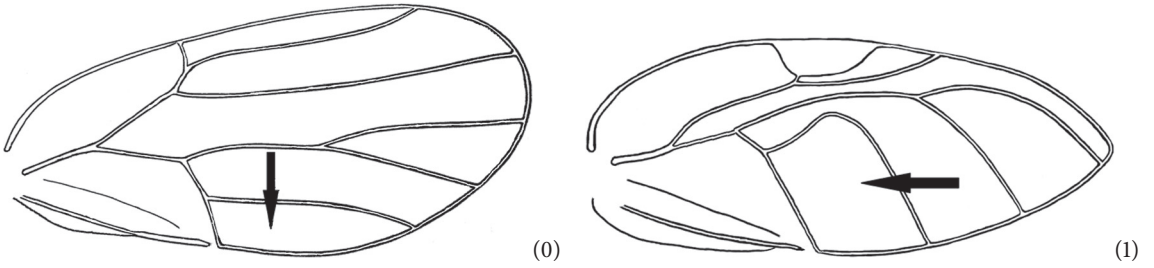
71. Cell m_1 of forewing narrow (0); cell m_1 wide (1) [Burckhardt, Lauterer 1997].



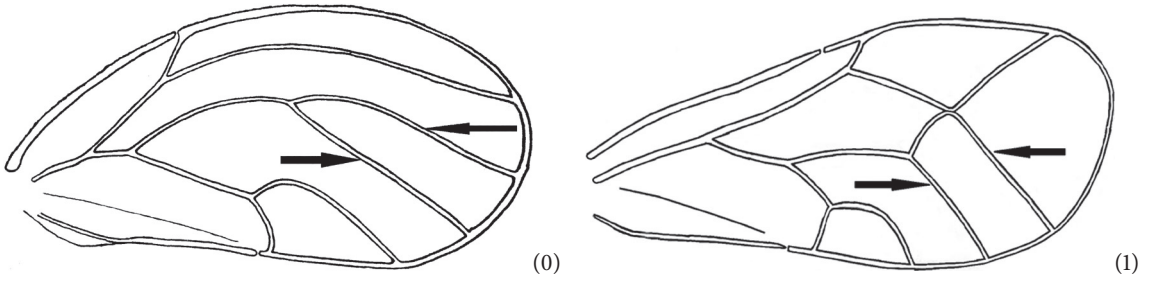
72. Cell r_1 long, narrow (0); cell r_1 short, broad (1) [Burckhardt 1986].



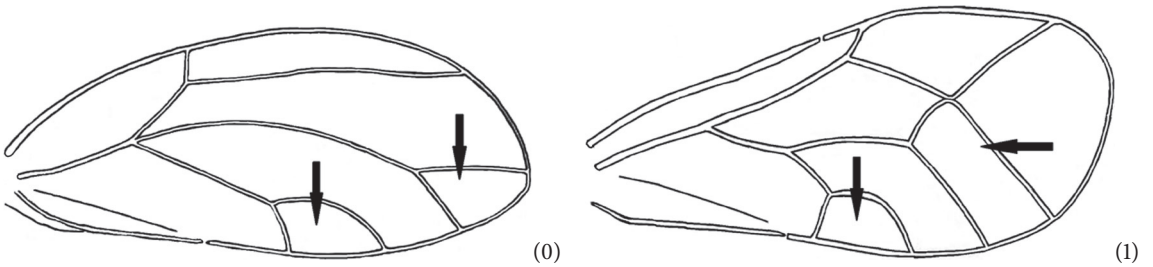
73. Cell cu_1 longer than higher (0); cell cu_1 higher than longer (1).



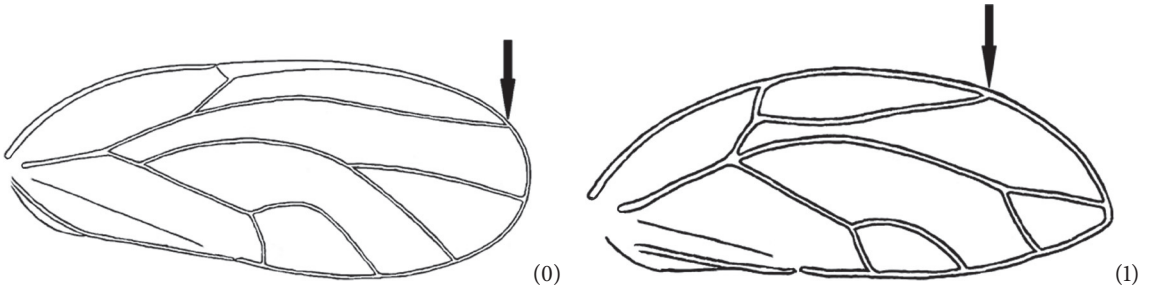
74. Vein M_{1+2} almost as long as vein M_{3+4} (0); vein M_{1+2} distinctly longer or shorter than M_{3+4} (1).



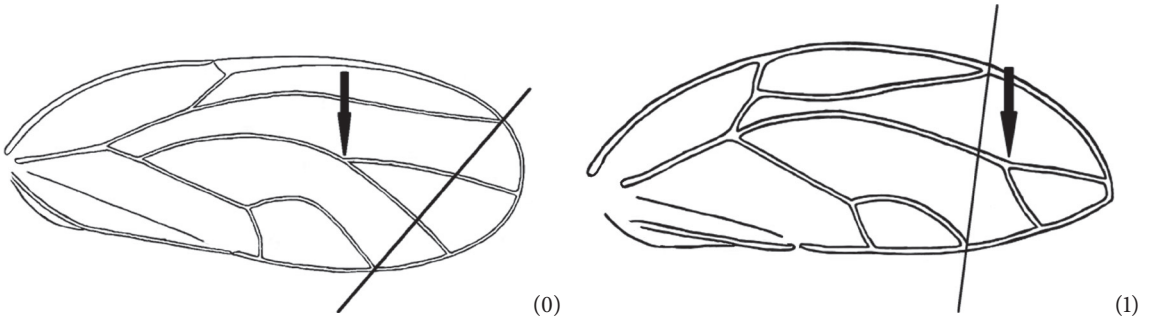
75. Cell m_1 the same size as cell cu_1 (0); cell m_1 not the same size as cell cu_1 (1) [Tuthill, Taylor 1955].



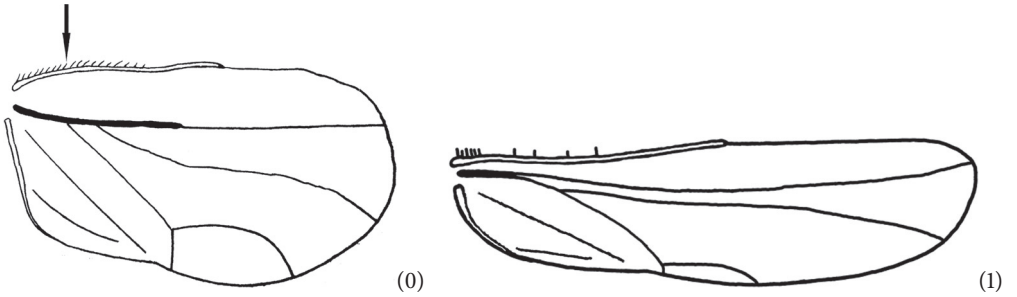
76. Vein Rs reaching almost to apex of wing (0); vein Rs not reaching to apex of wing (1).



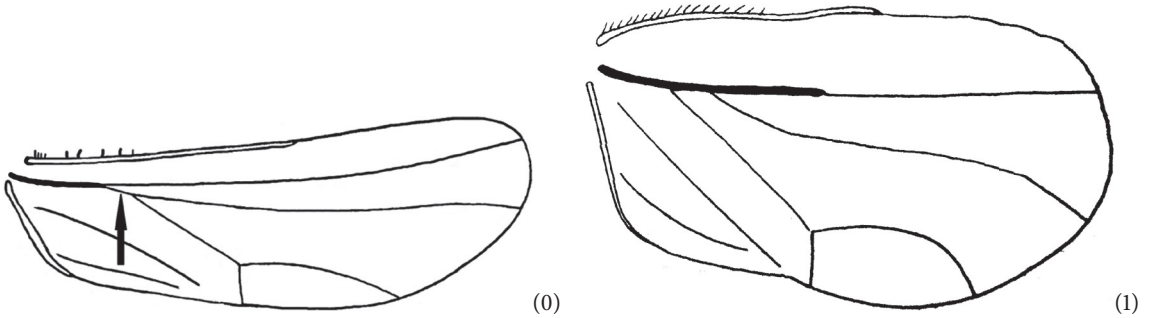
77. Vein M branching proximal to Rs-Cu_{1a} line (0); vein M branching distally to Rs-Cu_{1a} line (1) [Hollis 1984].



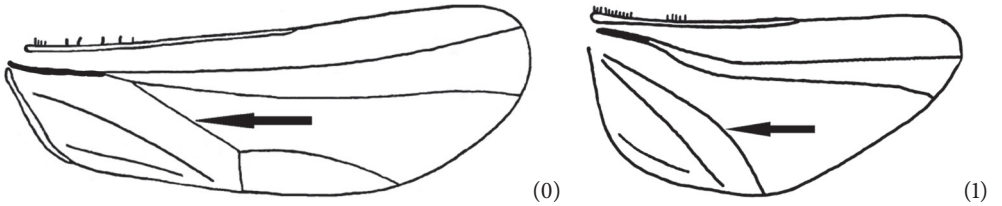
78. Costal setae of hindwing ungrouped (0); costal setae of hindwing grouped (1) [Hollis 1976].



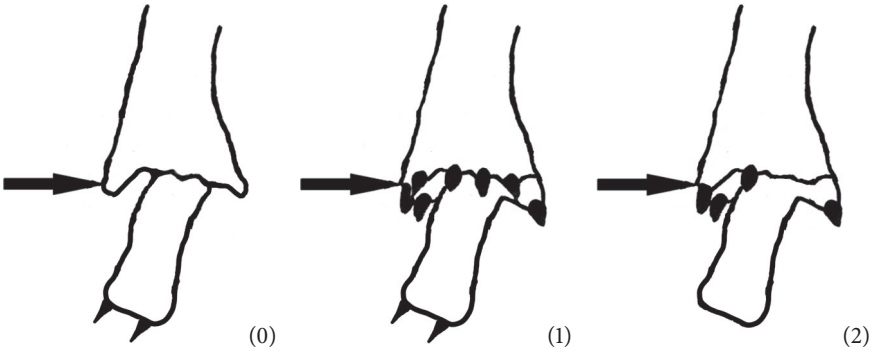
79. Hindwing with distinct M+Cu_1 (0); hindwing without M+Cu_1 (1) [Burckhardt, Basset 2000].



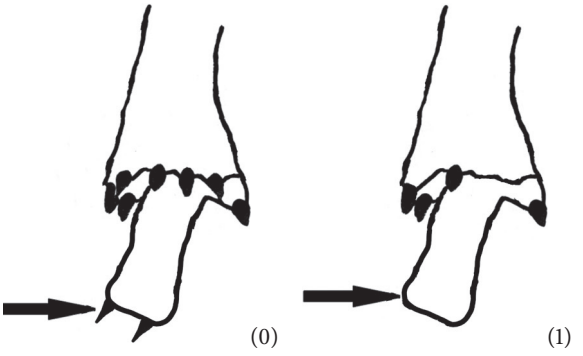
80. Cu of hindwing branched (0); Cu of hindwing unbranched (1) [Hollis, Broomfield 1989].



81. Metatibia lacking strongly sclerotized apical spurs (0); metatibia with an open crown of strongly sclerotized apical spurs (1); metatibia with an grouped apical spurs (2) [Hollis, Broomfield 1989 modified].



82. Metatarsal spurs present (0); metatarsal spurs absent (1) [White, Hodkinson 1985; Burckhardt, Ouvrard 2006]



3.2. Results of the phylogenetic analysis of Psylloidea

Phylogenetic relations within the Psylloidea were studied with the use of cladistic analysis. The analysis encompassed 82 morphological characters of adult psyllids, including 50 characters of the thorax morphology and 32 characters of thorax appendages (forewings, hindwings and hind legs). All the characters of the thorax and their polarization have been listed in Table 3, while the characters of the thorax appendages including their polarization have been presented in Table 4. Among the 50 characters of the thorax morphology separated for the analysis, only 6 had been earlier used by other researchers (White, Hodkinson 1985; Hollis 1987; Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt, Basset 2000; Burckhardt 2008). The structures of individual thorax appendages, contrary to the structure of this tagma, have been described numerous times and 26 of the selected characters had been used in earlier cladistic analyses (White, Hodkinson 1985; Hollis 1976, 1984, 1987; Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt 1991; Burckhardt, Basset 2000; Burckhardt, Ouvrard 2001, 2006). The authors of the works which utilized the selected characters have been provided by each of the characters in Tables 3 and 4.

Insects representing the superfamily Aleyrodoidea and extinct psyllids of the family Liadopsyllidae have been selected as the external groups.

Four equally most parsimonious trees and a consensus tree (tree length, L = 514; consistency index, CI = 0.20; retention index, RI = 0.61) (Fig. 73) have been obtained as a result of the analyses conducted for all the characters of the thorax and the appendages of the thorax. The analysis has confirmed that the Psylloidea is a monophyletic group and has proven the monophyly of the families Carsidaridae, Homotomidae, Phacopteronidae, Psyllidae and Triozidae, based on a series of synapomorphies. The conducted analysis has not, however, confirmed the monophyly of the families Aphalaridae, Liviidae and Calophyidae which do not constitute separate clades.

The superfamily Psylloidea (clade A, Fig. 73) is a monophyletic group exhibiting six synapomorphies: **4(1)**: membranous area between head and thorax absent; **5(1)**: pronotum slightly narrower than head with compound eyes; **14(1)**: prosternum not visible, covered by forelegs and rostrum; **50(1)**: meracanthus present and horn-shaped; **56(1)**: costal margin of forewing curved; **81(1)**: metatibia with an open crown of strongly sclerotized apical spurs; and nine homoplastic characters: **22(1)**: mesoscutum width less than twice its length; **30(2)**: mesopleural sulcus almost horizontal; **39(1)**: pleurosternal suture hardly visible; **46(1)**: metascutellum trapezoidal; **55(0)**: costal break present; **64(1)**: forewing with a narrow vein C+Sc; **70(1)**: cell m_1 small; **73(1)**: cell cu_1 height exceeding its length; **77(1)**: vein M branching distally to the Rs-Cu_{1a} line.

The conducted cladistic analysis has indicated that the family Carsidaridae (clade R, Fig. 73) is a monophyletic group, which is confirmed by two synapomorphies – **2(2)**: dorsal margin of thorax almost straight; **52(1)**: crossvein between veins Rs and M present. The remaining nine characters grouping the species of that family are homoplastic: **1(1)**: head weakly inclined in longitudinal body axis 0–45°; **8(0)**: lateral part of pronotum separated by weak-developed incision, lateral part not protruding anteriad; **13(1)**: propleurites narrow, lateral; **18(0)**: mesopraescutum length less than 3 times the length of pronotum; **26(0)**: mesoscutum distinctly separated from mesoscutellum, well visible; **36(1)**: transepimeral sulcus hardly visible; **40(0)**: basisternum rhomboidal; **43(1)**: metascutum not visible in dorsal view; **77(0)**: vein M branching near the Rs-Cu_{1a} line. The nine final states of characters also appear in other taxa and have seemingly developed in an independent manner.

The species of the Homotomidae (clade S, Fig. 73) constitute a monophyletic group based on two synapomorphies: **54(1)**: Cu_1 stem absent or very short and the character **80(1)**: Cu of hindwing unbranched. The remaining characters grouping these species into a single clade also occur in other taxa and are homoplastic: **3(1)**:

integument of thorax densely delicate setose; **15(1)**: two additional sclerites visible; **47(2)**: pair of tubercles present at metapostnotum; **69(1)**: vein Cu_{1a} weakly convex or almost straight; **73(0)**: cu_1 cell longer than its height; **75(0)**: m_1 cell of the same size as the cu_1 cell; **79(1)**: hindwing without M+Cu_1. Within the Homotomidae family (clade S, Fig. 73), the *Homotoma ficus* of the subfamily Homotominae is a sister species in relation to other species. It is a species which exhibits five apomorphic characters in relation to other species placed in that family: **12(2)**: propleural sulcus dorsally terminating at posterior angle of pronotum, **40(3)**: shape of basisternum indistinct, **48(1)**: trochantin on metathorax tuberculated, **59(1)**: M_{1+2} reaching wing margin before the apex of wing, **72(1)**: r_1 cell short, broad. Two of its characters exhibit reversion: **55(0)**: costal break present; **68(0)**: M_{1+2} vein curved backwards. Among the remaining species of the Homotomidae, the *Triozamia lamborni* of the subfamily Dynopsyllinae is a sister species of all the species classified in the subfamily Macrohomotominae (clade S, Fig. 73), exhibiting ten autapomorphic characters – **7(1)**: pronotum longer or shorter along the mid-line than along lateral portions; **19(1)**: mesopraescutum indistinctly separated from mesoscutum; **21(1)**: mesoscutum width less than twice its length; **22(2)**: F/G ratio on mesoscutum amounting to ~1.5; **28(3)**: U-shaped mesoscutellum; **33(1)**: parapteron not oval; **43(1)**: metascutum not visible in dorsal view; **51(1)**: R+M+Cu_1vein trifurcate, giving rise to R, M and Cu_1; **67(1)**: Rs vein curved in forward direction; **82(1)**: metatarsal spurs absent. The species of the Macrohomotominae (clade S, Fig. 73) form a group based on three homoplasies: **12(1)**: propleural sulcus dorsally terminating at anterior angle of pronotum; **16(1)**: mesopraescutum as wide as pronotum; **31(1)**: anapleural cleft distinct, oblique and /(or) short; and two characters exhibiting reversion: **46(0)**: metascutellum rectangular; **63(0)**: pterostigma present. The two latter characters have returned to their initial state.

The species of the families Triozidae and Phacopteronidae form a common T clade (Fig. 73) based on five homoplasies: **5(2)**: pronotum distinctly narrower than head with compound eyes; **10(1)**: pronotum vertically or subvertically inclined and often completely or partially concealed by head; **28(2)**: mesoscutellum U-shaped; **40(3)**: basisternum triangular; **79(1)**: hindwing without M+Cu_1. In that clade (clade T, Fig. 73), the Phacopteronidae are a sister group of the Triozidae family species. The Phacopteronidae are characterized by four autapomorphies – **53(1)**: Rs and M_{1+2} veins in contact and forming a cross; **57(1)**: costal margin in distance of pterostigma; **56(0)**: costal margin not curved; **81(0)**: metatibia lacking strongly sclerotized apical spurs; and ten homoplastic characters: **8(0)**: lateral part of pronotum separated by weakly-developed incision, lateral part not protruding anteriad; **9(1)**: posterior margin of pronotum slightly arched, with incision; **11(0)**: proepisternum and proepimeron of the same size; **13(0)**: propleurites broad, lateral; **46(0)**: metascutellum rectangular; **55(0)**: costal break present; **64(0)**: forewings without narrow C+Sc vein; **70(1)**: cell m_1 small; **71(0)**: cell m_1 of forewing narrow; **72(1)**: cell r_1 short, broad.

The species of the family Triozidae (clade U, Fig. 73) form a monophyletic group based on four synapomorphies **6(2)**: anterior margin of pronotum U-shaped; **8(2)**: lateral part separated by well-developed incision, lateral part protruding anteriad; **58(1)**: anal break in distance of apex of Cu_{1b} vein; and **17(1)**: mesopraescutum width lower than length. The species of that family exhibit many homoplastic characters: **7(1)**: pronotum longer or shorter along the mid-line than along lateral portions; **12(2)**: propleural sulcus dorsally terminating at posterior angle of pronotum; **20(2)**: anterior margin of mesoscutum U-shaped; **26(0)**: mesoscutum distinctly separated from mesoscutellum, well visible; **31(1)**: anapleural cleft distinct, oblique and (or) short; **37(1)**: tubercle of trochantin before mesocoxa present; **42(0)**: anterior protrusions of katepisternum present as small, oval structures; **44(1):** metascutellum as wide as mesoscutellum; **48(1)**: trochantin on metathorax tuberculated; **51(1)**: vein R+M+Cu_1 trifurcate, giving rise to R, M and Cu_1;. **56(1)**: costal margin curved; **59(1)**: M_{1+2} reaching wing margin before the apex of wing; **61(1)**: forewing apically angular; **75(0)**:

cell m_1 of the same size as the cell cu_1; **77(0)**: vein M branching near the Rs-Cu_{1a} line; **82(1)**: metatarsal spurs absent. Within that clade, the species *Bactericera bielawskii* is a sister group of other species due to the reversion of the **17(0)** character, that is, mesopraescutum width greater than its length, while in the remaining species of that family, its length always exceeds the width **17(1)**. Another sister species of the Triozidae in concern is the *Trioza galii* which exhibits the reversion of the **67(0)** character, that is the Rs vein nearly reaching the apex of the wing, while the vein is shortened in the remaining species **67(1)**. The dichotomous branching of that clade consists in homoplasies. The first clade, including the *Trichochermes walkeri, Egeirotrioza ceardi* and *Trioza malloticola* species is distinguished based on the following characters: **3(1)**: integument of thorax densely covered with delicate setae and **75(1)**: cell m_1 of different size than the cell cu_1; while the second, including the *Bactericera curvatinervis*, *Calinda pehuenche, Trioza anthrisci, Trioza berberidis* is distinguished base on the character **77(1)**: vein M branching distally to Rs-Cu_{1a} line.

The analyzed species of the Psyllidae (clade M, Fig. 73) constitute a single clade based on just one synapomorphy: **13(1)**: propleurites narrow, lateral; and three homoplastic characters: **11(0)**: proepisternum and proepimeron of the same size; **30(0)**: mesopleural sulcus long, distinct and oblique; **81(2)**: metatibia with grouped apical spurs. Within that clade, the *Ephyllerus vittatus* of the subfamily Macrocorsinae is a sister species of all the remaining Psyllidae and is distinguished by means of three apomorphies: **42(2)**: anterior protrusions of katepisternum present as structures with a sharp point; **43(1)**: metascutum not visible in dorsal view; **46(1)**: metascutellum trapezoidal; and one reversion – **31(0)**: anapleural cleft (acl2) distinct, almost horizontal and long. The remaining species of the Psyllidae are combined into a single group based on a single apomorphy – **29(1)**: posterior margin of mesoscutellum with incision in middle. Within that family, the species of the subfamilies Acizzinae, Aphalaroidinae and Ciriacreminae constitute a single clade based on four homoplasies – **11(1)**: proepisternum and proepimeron not equal in size; **29(0)**: straight posterior margin of mesoscutellum without central incision; **30(2)**: mesopleural sulcus nearly horizontal and **31(0)**: anapleural cleft (acl2) distinct, almost horizontal and long. The species of the Ciriacreminae have been combined based on two characters – a reversion: **12(0)**: propleural sulcus dorsally terminating at mid-point of pronotal lateral margin; and an apomorphy – **32(1)**: pleural sulcus connected with anapleural cleft, a character also present in just one analyzed species of the Liviidae family, *Glycaspis brimblecomblei*. The sister group of the Ciriacreminae is subfamily Aphalaroidinae, with which they constitute a group sharing one character exhibiting reversion: **24(0)**: mesoscutum up to 1.5 times wider than mesopraescutum. In the Psyllinae, the *Anomoneura mori* and *Arytaina maculata* are sister species which are characterized by the the mid-line of the pronotum being longer than its lateral parts **7(1)**.

All the families of the Psylloidea referred to above were combined into clades which indicate at least one synapomorphic character. The species of the Liviidae family as understood by Burckhardt and Ouvrard (2012) do not constitute a monophyletic group based on the morphology of the thorax and its appendages. Four analyzed species of the Liviinae subfamily have been grouped based on six characters. All of these characters, however, are homoplastic: **7(1)**: pronotum longer or shorter along the mid-line than along lateral portions; **39(0)**: pleurosternal suture well visible; **49(0)**: pleural sulcus on metathorax visible; **65(0)**: vein R as long as the vein M+Cu_1; **67(0)**: vein Rs straight or curved backwards; **75(0)**: cell m_1 of the same size as the cell cu_1. Along with the *Calophya rhois* species, classified as a member of the Calophyidae, they constitute a single clade (clade N, Fig. 73). The clade, however, is supported only by the presence of homoplasies: **12(2)**: propleural sulcus dorsally terminating at posterior angle of pronotum; **34(1)**: parapteron and tegula of the same size and **82(1)**: metatarsal spurs absent. The species of the subfamily Euphyllurinae (Liviidae) also do not exhibit synapomorphy of the morphology of thorax and its appendages.

Some of them (Pachypsylloidini, Euphyllurini and Strophingiini) constitute a common clade, but the clade is supported by homoplastic characters only: **13(3)**: propleurites displaced ventrally; **46(1)**: metascutellum trapezoidal and **65(0)**: vein R as long as the vein M+Cu_1. The species constitute a common clade (clade J, Fig. 73) with the species of the subfamilies Rhinocolinae and Togepsyllinae (Aphalaridae), based, however, on three homoplasies: **8(0)**: lateral part of pronotum separated by weakly-developed incision, lateral part not protruding anteriad; **12(1)**: propleural sulcus dorsally terminating at anterior angle of pronotum; **23(1)**: mesoscutum 1.5 times longer than mesopraescutum along the mid-line. The remaining two species of the Euphyllurinae, tribe Diaphorinini, are separated. *Diaphorina truncata* takes the position of the sister species in relation to the species described earlier (clade H, Fig. 73), while the *Psyllopsis fraxinicola* forms a common clade with the Psyllidae family (clade K, Fig. 73). This clade, however, is only supported by four homoplastic characters: **5(2)**: pronotum distinctly narrower than head with compound eyes; **18(1)**: mesopraescutum more than 3 times longer than pronotum along the mid-line; **37(1)**: tubercle of trochantin anteriorly of mesocoxa present; **48(1)**: trochantin on metathorax tuberculated.

The conducted cladistic analysis based on the characters of the morphology of thorax and its appendages has not confirmed that the family Aphalaridae as understood by Burckhardt and Ouvrard (2012) is a monophyletic group. The species of the subfamily Spondyliaspidinae constitute a common clade based on five homoplasies: **38(0)**: anterior margin of mesosternum straight, without incision; **49(1)**: pleural sulcus on metathorax not visible, **50(0)**: meracanthus absent, **74(1)**: vein M_{1+2} distinctly longer or shorter than M_{3+4} ; **81(2)**: metatibia with grouped apical spurs. The *Xenaphalara signata* of the subfamily Aphalarinae (Aphalaridae) constitutes a common group with the species of the subfamily Spondyliaspidinae, however, it is based only on homoplasy: **8(1)**: lateral part separated by well-developed incision, lateral part not protruding anteriad; **11(1)**: proepisternum and proepimeron not subequal and **41(1)**: lateral part of katepisternum at ventral side wider than the width of head with eyes. One of the species of the Pachypsyllinae (Aphalaridae), the *Pachypsylla venusta*, constitutes a common group with the *Cecidopsylla schimae* of the family Calophyidae (clade F, Fig. 73), based on the following homoplasies: **13(2)**: propleurites displaced antero-ventrally; **41(1)**: lateral part of katepisternum at ventral side wider than width of head with eyes; **47(2)**: pair of tubercles present on metapostnotum and **73(0)**: cell cu_1 length exceeding its height; **79(1)**: hindwing without M+Cu_1. The remaining species of the Calophyidae – *Bharatriana octospinosa* and *Mastigimas reseri* do not exhibit synapomorphies. The *Mastigimas reseri* takes the position of a sister species for the clade encompassing the species of the families Carsidaridae, Homotomidae, Phacopteronidae and Triozidae (clade O, Fig. 73), while the *Bharatiana octospinosa* is a sister species of all the species referred to above, including *Mastigimas reseri*.

When comparing the structure of the individual trees (Figs. 74–77) with the consensus tree (Fig. 73), a high stability of taxa may be noted, with the exception of four species classified in the families Apahalaridae and Psyllidae. The instability is exhibited by the following species: *Craspedolepta sonchii* and *Colposcenia jakowleffi* of the Aphalaridae (yellow area, Figs. 74–77) and *Psylla foersteri* and *Cyamophila bajeva* of the Psyllidae (green area, Figs. 74–77). These changes only consist in homoplasies. The remaining species maintain unchanged positions in all created cladograms.

4 Discussion

The presented work includes a description of numerous new external morphological characters of the thorax structure in 59 species of psyllids representing all families and nearly all subfamilies (with the exception of Atmetocraniinae, Metapsyllinae and Symphorosinae) in concordance with the classification compiled by Burckhardt and Ouvrard (2012). The respective thorax structures have been described, unified and compared in the analyzed species. The previous information regarding the thorax morphology of psyllids were dispersed across many publications and contained a series of inaccuracies and discrepancies regarding the description of the individual structures – starting with the work by Stough (1910), in which the author described the additional anterior sclerite as the proepimeron, through the interpretation by Heslop-Harrison (1952), who described the fossa of the trochantinal apodeme (ftna2) as the mesothoracic spiracle, and ending with Journet and Vickery (1978), who additionally suggested that the mesothoracic spiracle is the spiracle of the prothorax and described the transepimeral sulcus as the pleural sulcus at the mesothorax. That same misinterpretation of the transepimeral sulcus as the pleural sulcus occurs in the works by Matsuda (1970, 1979). Ouvrard et al. (2002), however, proved that the sulcus does not exhibit internal pleural apophysis and should be regarded as a second sulcus at the mesothorax. Matsuda (1970) also described the course of the anapleural cleft as much higher than the factual course, which has been verified by Ouvrard et al. (2002), who have proven that the course of the anapleural cleft is notably more ventral. The determination whether sclerites are present between the head and the pronotum or the head directly touches the pronotum, was also problematic. According to Taylor (1918), 3 pairs of cervical sclerites exist between the head and the pronotum (*pronotum*, nt1) – in the so-called collar region of insects earlier classified as members of the Homoptera group. Matsuda (1970, 1979) demonstrated that Taylor was not right and that among all the insects earlier classified as Homoptera, only the Cicadidae have such sclerites. Weber (1929), on the other hand, described two such highly reduced sclerites in *Psylla mali*. Ouvrard et al. (2002), however, proved that one of them had been mistaken with the extension of the proepisternum, while the second one was beyond doubt the trochantin. The results of the analyses of the area between the head and the pronotum of psyllids indicate that no additional sclerites are present (Heslop-Harrison 1951; Ouvrard et al. 2002; Drohojowska 2009a, b, 2013). No sclerites between the head and the prothorax have been found in the course of the presented research. The last work presenting the data regarding the thorax in pyllids (Li 2011) includes many structures lacking description, such as e.g. the prealar bridge, the anterior and posterior additional sclerite as well as structures that had been described incorrectly such as the tegula or fossa of the pleural apophysis, which had been described as the mesostigma. This caused the number of stigma at the peritremes to be incor-

rect. In many works, the same morphological structures of the thorax had been given various terms. A list of the names and their unification has been presented by Ouvrard et al. (2002).

In several earlier works based on the morphology of adult insects, cladistic analysis methods were used to determine the phylogenetic relations within various taxonomic units of psyllids (White, Hodkinson 1985; Hollis 1976, 1984, 1987; Burckhardt, Lauterer 1989; Hollis, Broomfield 1989; Burckhardt 1991; Burckhardt, Basset 2000; Burckhardt, Ouvrard 2001, 2006, Burckhardt 2008). In their analyses, the authors of these works have used over 260 morphological characters, partially overlapping in terms of their scope. All the characters have been polarized, although often the polarization differed – e.g. the pterostigma development in forewings was in some cases regarded as a plesiomorphic character (White, Hodkinson 1985; Hollis 1987; Burckhardt, Lauterer 1989), while being considered an apomorphic character by others (Hollis, Broomfield 1989). Other examples include the anal cone in males regarded as a plesiomorphic state (Hollis 1987; Burckhardt, Lauterer 1989; Hollis, Broomfield 1989) or an apomorphic state (White, Hodkinson 1985). A part of the proposed polarizations had to be changed in view of the data obtained from the fossil material. This is exemplified by the assumption made by Hollis (1987) that the covering of the body with long thick setae is a plesiomorphic state, while the presence of delicate sparse setae covering the body in psyllids, or the lack thereof, is an apomorphic state. No setae is observed in all Liadopsyllidae and Malmopsyllidae, so the polarization proposed by Hollis (1987) has been changed.

This research utilized 51 new characters that have not been used in earlier works, while 10 out of the previously used characters were modified. In a few cases, the polarization of characters has been changed. Because the characters used by earlier researchers were mostly used for determining the relations within genera, and less often within larger taxa, the authors of these studies have mostly selected and determined characters that were variable within a genus. The use of these characters for determinations at the level of families, subfamilies and tribes was not possible. In the presented research, only such characters have been selected that are characteristic to genera and invariable in all species within a genus.

According to opinion of Burckhardt and Ouvrard (2012), it is impossible to create a clear and up-to-date classification of the world fauna of the superfamily Psylloidea based on the contemporary incomplete knowledge of the phylogeny of psyllids. Each additional study, however, both morphological and molecular, covering the characters of adult insects or nymphs, expands our knowledge of the phylogeny of psyllids and brings the researchers closer to creating such a classification.

Based on a cladistic and phenetic analysis of the morphological characters of nymphs and adult insects, White and Hodkinson (1985) created a classification of psyllids occurring all over the world. Many subsequent analyses based on the morphological characters and molecular studies tested, modified and expanded their classification (Hollis 1985, 1987; Burckhardt 1987a, b, 1988, 1991; Hollis, Broomfield 1989; Burckhardt, Lauterer 1989, 1997a, b; Klimaszewski 1993b, 2001; Hollis, Martin 1997; Burckhardt, Basset 2000; Thao et al. 2000; Ouvrard 2002; Burckhardt, Mifsud 2003; Percy 2003b; Ouvrard, Burckhardt 2008; Li 2011). There were differences among many of these classifications (Burckhardt, Ouvrard 2012). The last presented classification of psyllids proposed by Burckhardt and Ouvrard (2012) was an attempt to combine the knowledge of the phylogeny of psyllids in the creation of a general classification comprising of monophyletic groups, that the authors have proposed based on useful information obtained in other works and unpublished data from continued morphological and molecular studies covering the world fauna of psyllids (Burckhardt, Ouvrard 2012). The authors have not presented any new results but rather relied on published morphology-based revisions of individual taxonomic units (Burckhardt 1987a, 1991, 2005; Burckhardt, Basset 2000; Burckhardt, Lauterer 1989, 1997a, b; Burckhardt, Mifsud 2003; Hollis 1985, 1987;

Hollis, Broomfield 1989; Hollis, Martin 1997) and hitherto unpublished molecular studies conducted by David Ouvrard (Burckhardt, Ouvrard 2012). The authors have presented their conclusions drawn based on phylogeny deliberations in the form of a diagram including all families and subfamilies distinguished within the Psylloidea.

The authors have created eight families within the superfamily Psylloidea (Aphalaridae, Calyophyidae, Carsidaridae, Homotomidae, Liviidae, Phacopteronidae, Psyllidae, Triozidae), six of which corresponded to the families of the earlier classification by White and Hodkinson (1985) to some extent. As the Aphalaridae and Spondyliaspididae, *sensu* White and Hodkinson (1985) were regarded as polyphyletic (Burckhardt 1987a, 1991; Burckhardt, Ouvrard 2012) or paraphyletic (White, Hodkinson 1985) their scope was largely modified by Burckhardt and Ouvrard (2012).

In the presented research, the results obtained based on analyses of morphological characters of the thorax and its appendages indicate phylogenetic relations within the Psylloidea superfamily largely corresponding to those proposed by Burckhardt and Ouvrard (2012).

The Aphalaridae *sensu* Burckhardt and Ouvrard (2012) is comprised of species classified as members of five probably monophyletic subfamilies (Burckhardt, Ouvrard 2012). The diagnosis of species representing the Aphalaridae *sensu* Burckhardt and Ouvrard (2012), encompasses two characters – one concerns the possession of metatibia with an open crown of sclerotized apical spurs (sometimes grouped) by imaginal forms, while the second concerns the nymphs and their possession (or lack thereof) of an arolium plate on the tarsus without an unguitractor. Moreover, the authors provided that the species of three subfamilies: Rhinocolinae, Spondyliaspidinae and Togepsyllinae are characterized by synapomorphy – the lack of a horn-shaped meracanthus (sometimes they have a tuberculated or spherical meracanthus). In the Aphalarinae and Pachypsyllinae, the meracanthus is well developed and horn-shaped. The conducted research confirmed the lack of a horn-shaped meracanthus in the subfamilies Rhinocolinae, Spondyliaspidinae and Togepsyllinae. However, that state of the character has been assumed to be plesiomorphic. If, as provided by Ouvrard et al. (2010), the extinct species of the Liadopsyllidae family exhibited no meracanthus or the meracanthus was small and these species had no capability to jump, the development of a large horn-shaped meracanthus and the acquisition of jumping capabilities may be regarded as apomorphy. Thus, the presence of a small meracanthus or the lack thereof in the subfamilies referred to above may not be regarded as synapomorphy, but rather a symplesiomorphy or a character exhibiting reversion. In none of the analyzed species of the Aphalaridae *sensu* Burckhardt and Ouvrard (2012), the thorax is separated from the head by a membranous area, whereas the anterior margin of the pronotum is arched. Among the Aphalaridae, a wider mesothorax is observed, within which the width of the mesopraescutum always exceeds its length and the mesoscutum's width is over twice its length. In the species of that family, the mesoscutellum is devoid of the incision at the posterior margin and its width is over twice the width of the metascutellum, which does not cover the metascutum. The metascutum remains well visible in the dorsal view. All the mentioned characters, common to the species of the Aphalaridae *sensu* Burckhardt and Ouvrard (2012), also occur in some of the species of the remaining families and thus they may not be regarded as synapomorphies. The conducted research has not indicated any characters in the thorax morphology that would evidence the monophyly of the Aphalaridae *sensu* Burckhardt and Ouvrard (2012). By distinguishing the family Aphalaridae in that respect, the authors suggested the probable monophyly of the five subfamilies that constitute the family (Burckhardt, Ouvrard 2012). Some of the characters of the appendages structure in the Aphalaridae species are also common to all the analyzed species. These include forewings with costal break near the vein R_1 and anal break near the vein Cu_{1b}, curved costal margin, dichotomous branching of the vein $R+M+Cu_1$, lack of connection between the

veins Rs and M, no contact between the Rs and M_{1+2} veins long Cu_1 vein. The wings of this family are the widest at 2/3 of the wing's length or at the middle, rounded at the ends with a vein M_{1+2} curved towards the front and a moderately curved vein Cu_{1a}. In the hindwings, the vein Cu is always branched and the metatarsal spurs are well developed, whereas the apical spurs at the tibia are also always well developed and form an open crown or groups. These characters are also not typical only to the species of the Aphalaridae, but also occur in other families. Based on these characters, it is impossible to confirm the monophyly of the Aphalaridae *sensu* Burckhardt and Ouvrard (2012). The monophyly of five subfamilies within the Aphalaridae family suggested by Burckhardt and Ouvrard (2012) also has not been confirmed based on the morphology of the thorax and its appendages. Despite the presence of many characters of the thorax and its appendages grouping the species from the particular subfamilies, there are no grounds for considering them as monophyletic.

The Calyophyidae, as classified by Burckhardt and Ouvrard (2012), includes the psyllid species which, presently combined into a single group, are impossible to diagnose. As these authors provided, the Calyophyidae comprise of five probably monophyletic subfamilies, yet no autapomorphies – neither morphological nor molecular – that would confirm the monophyly of this family have been found to date. The authors, however, suspect the probability that the five subfamilies comprising the family are monophyletic. According to these authors, the metatibia with an internal row of apical spurs and the lack of spurs at the basal part of the tarsus may evidence the close relationship of the subfamilies Atmetocraniinae, Calyophyinae and Metapsyllinae. In the conducted study of the morphology of the thorax and its appendages, the species of three monotypic subfamilies: Atmetocraniinae, Metapsyllinae and Symphrosinae, have not been analyzed. The insects selected for the analyses were the representatives of the Calophyinae – *Calophya rhois* and as many as three representatives of the Mastigimatinae: *Bharatiana octospinosa, Cecidopsylla schimae* and *Mastigimas reseri*. The species of both the mentioned subfamilies exhibited as much as 65% of common character states (54 of 82 analyzed characters) and not a single character that would be an autopomorphy indicating their relationship. In all the cladograms (Figs. 73–77), the *Cecidopsylla schimae* exhibits greater affinity in relation to the *Pachypsylla ventusta* of the Aphalarinae than with the species with which it shares the Mastigimatinae *sensu* Burckhardt and Ouvrard (2012). The *Calophya rhois* of the Calophyinae exhibits greater affinity with the species of the Liviinae (clade N, Fig. 73) than with the other species of the Calophyidae. Based on the conducted analyses, the monophyly of the family Calophyinae may not be confirmed. It is also impossible to confirm the monophyly in the analyzed subfamilies Calophyinae and Mastigimatinae, *sensu* Burckhardt and Ouvrard (2012). The typical characters of the thorax in the analyzed species of the Calophyinae were its slight arching, the direct contact of the pronotum and the head, where the pronotum is slightly narrower than the head including the eyes. In that group of species, the pronotum is characterized by an arched anterior and posterior margin and by its similar length at its mid-line and at its lateral portions, where slight cavities occur. Among the species of the Calophyidae, propleurites of variable sizes and their displacement in the anteroventral direction is observed. In the Calophyidae, all three additional pleurites are visible. Their mesopraescutum is narrower than the pronotum, and its width exceeds its length. It is also distinctly separated from the mesoscutum, while the posterior mesopraescutum suture is arched. The width of the mesoscutum in the Calophyidae is more than twice its length, while in its mid-line, the mesoscutum is longer or slightly longer than the mesopraescutum. The mesoscutellum in the Calophyidae forms the shape of a wide trapezoid an it is 2.5 times narrower than the mesoscutum and nearly twice the width of the metascutellum. The mesopleural sulcus and the anapleural cleft in the species of that family do not touch each other, while the parapteron and tegula are always oval. While analyzing the ventral side of the thorax in the species of

the Calophyidae, no convexity is observed on the trochantin in front of the mesocoxa; the anterior margin of the mesosternum exhibits a central incision, while the pleurosternal suture is barely visible. The species of the Calophyidae have maintained a metascutum that is visible in the dorsal view, while the pleural sulcus is not visible at the metathorax, the trochantin is not tubercular and the meracanthus is large and horn-shaped.

The family Carsidaridae, Crawford 1911, has been diagnosed and analyzed using cladistic methods by Hollis (1987). He has not distinguished subfamilies or tribes within that family. According to Hollis (1987), it is a monophyletic family exhibiting two characters: a supplementary lobe on the male subgenital plate and the presence of non-traechate Rs-M crossvein in the forewing. In the presented research, the presence of the Rs-M crossvein and a nearly straight, little arched dorsal margin of the thorax have been confirmed only in the species of the Carsidaridae and that characters have also been recognized as synapomorphies, thus confirming the monophyletic nature of the family. In terms of thorax morphology, the species of the Carsidaridae are characterized by and the pronotum slightly narrower than the width of the head with eyes. In Carsidaridae, an arched anterior margin of the pronotum is observed. The length of the pronotum is similar in its mid-line and lateral portions, where small cavities are observed. The proplerutites of the Carsidaridae species are of the same size and the sulcus separating the propleurites reaches the middle of the lateral margin of the pronotum. All three additional sclerites are visible in that group of species. Among the Carsidaridae, the mesothorax narrows in relation to the prothorax, the mesopraescutum is narrower than the pronotum and its width exceeds its length. The mesopraescutum of the Carsidaridae is also distinctly separated from the mesoscutum and the separating element is U-shaped. In that family, the extension of the mesoscutum in relation to the mesopraescutum and a distinct separation of the mesoscutum and the mesoscutellum occurred. The mesopleural sulcus of the Carsidaridae species is long and distinct. Its course is diagonal and it does not reach the anapleural cleft, which is distinct, nearly horizontal and long. The Carsidaridae exhibit a parapteron larger than the tegula, while both the structures are oval and easily noticeable – contrary to the transepimeral sulcus, which is barely visible. The ventral side of the mesothorax in the Carsidaridae is characterized by the lack of a trochantin convexity in front of the mesocoxa, an incision in the anterior margin of the mesosternum and the lateral portions of the katepisternum exceeding the width of the head including the eyes. Moreover, in the Carsidaridae the pleurosternal sulcus is well visible and the basisternum is rhomboidal. The metascutum is not visible in the species of that family and the trapezoidal metascutellum touches the mesoscutellum. The metascutellum is half the width of the mesoscutellum and shorter in the central line. The metapostnotum of the Carsidaridae contains a single spur in the middle, and the metathoracic trochantin is not convex. The pleural sulcus at metathorax is not visible, although a horn-shaped meracanthus is easily noticeable in all the species of the Carsidaridae.

The Homotomidae *sensu* Hollis and Broomfield (1989) was well diagnosed and analysed. The authors treated it as a monophyletic group and distinguished three subfamilies: Dynopsyllinae, Homotominae and Macrohomotominae. The presented research confirms the monophyly of that family, which is supported by two synapomorphies – the vein Cu_1 is very short or inexistent and the non-branching vein Cu, and many apomorphies such as the delicate setae on the thorax, two additional sclerites visible, the presence of two convexities at the metapostnotum, a slightly convex or nearly straight vein Cu_{1a} the length of the cu_1 exceeding its height, the m_1 and cu_1 cells of the same height, the lack of the vein $M+Cu_1$ at the hind wing. The species of the Homotomidae family are characterized by a slightly arched thorax with a slightly arched posterior margin of the pronotum. In these species, the mesoscutum as long as the mesopraescutum measured in the central line or slightly longer and delicately separated from the mesoscutellum is preserved. In the species of the Homotomidae, the mesopleural sulcus is

distinct, long and diagonal. It does not reach the anapleural cleft. In that group, the parapteron may assume various shapes, but the tegula is always oval and smaller than the parapteron. The species of the Homotomidae family are also characterized by the metascutellum being shorter than the mesoscutellum measured in the mid-line and the invisible pleural sulcus at the metathorax, as opposed to the distinct, large horn-shaped meracanthus.

According to earlier analyses, the species of the families Carsidaridae and Homotomidae are closely related (clade P, Fig. 73), which had been earlier suggested by researchers who based their analyses on other characters (Hollis 1987; Hollis, Broomfield 1989; Burckhardt, Ouvrard 2012). According to Hollis (1987), the species are related by common apomorphies – a pair of tubercles at the metapostnotum and the characteristic arrangement of sense organs at the hind femur. The provided apomorphies may also include the formation of a second distinct and diagonal mesopleural sulcus and the lateral portions of the katepisternum exceeding the width of the head.

The family Liviidae *sensu* Burckhardt and Ouvrard (2012), was distinguished based on the presence of an open row of sclerotized spurs (sometimes grouped) at the metatibia and the fact that larvae most often exhibit multiple lanceolate setae or sectasetae and a tarsal arolium bearing unguitractor. According to Burckhardt and Ouvrard (2012), the family is comprised of two probably monophyletic subfamilies: Liviinae and Euphyllurinae. The presented research has not provided any evidence for the monophyly of the Liviidae or the monophyly in any of its two subfamilies. The species of that family do not exhibit common synapomorphies, while the morphology of their thorax is characterized by a slightly arched posterior margin of the pronotum that is free of any incision. The pleurites of the prothorax – the proepisternum and the proepimeron assume various sizes in the Liviidae. The mesopraescutum is narrower than the pronotum, while its width exceeds its length in the dorsal view. In the species of the Liviidae, the mesoscutum is very wide, reaching over twice its length, while the mesoscutellum is 2.5 times narrower than the mesoscutum. The posterior margin of the mesoscutellum is straight and free of incisions. In the species of this family, the course of the pleural sulcus varies but it never touches the anapleural cleft. The dorsal side of the Lividae is additionally characterized by an incison in the middle of the anterior margin of the mesosternum, a visible metascutum and a metascutellum shorter than the mesoscutellum in its midline. Moreover, the species of the Liviidae exhibit a well-visible horn-shaped meracanthus.

The Phacopteronidae Heslop-Harrison, 1958 family has been diagnosed by Heslop-Harrison (1958) and White and Hodkinson (1985) and it is comprised of five poorly diagnosed genera – four extant and one extinct (Burckhardt, Ouvrard 2012). The relations within that family have not yet been specified and no subfamilies or tribes have been distinguished. One representative of the *Pseudophacopteron zimmermanni* has been analyzed in the presented research. Four characters present only in that species have been distinguished: interconnected and crossing the veins Rs and M_{1+2}, straight costal margin, costal break distant from the vein R_1 and metatibia without sclerotized apical spurs.

The family Psyllidae *sensu* Burckhardt and Ouvrard (2012), was defined based on the developed horn-shaped meracanthus. The metatibia usually contains grouped apical spurs and the metabasitarsus is usually equipped with two lateral spurs. The nymphs of the species of that family exhibit a triangular petiolate tarsal arolium, often with capitate setae and sectasetae. The analyzed species of the Psyllidae exhibit a single synapomorphy – narrow lateral propleurites – and a series of common apomorphic and plesiomorphic characters resulting in their classification within one branch in the cladograms (Figs. 73–77). The body in all the species of the Psyllidae is characterized by the head strongly inclined downwards (45–90°). The dorsal side of the thorax is slightly arched in the lateral view. The pronotum of these species is distinctly narrower than the head with eyes and its anterior margin is arched. The lateral portions of the

pronotum exhibit well-developed cavities. Three additional sclerites are visible in Psyllidae. The mesopraescutum of the Psyllidae is narrower than the pronotum and its width exceeds its length. The anterior margin of the mesoscutum is arched and the width of the mesoscutum is over two times its length. In comparison with the mesopraescutum, the mesoscutum measured in the midline is of the same length or slightly longer, while the wide trapezoidal mesoscutellum is over 2.5 times narrower than the mesoscutum. The parapteron is larger than the tegula and both the structures exhibit an oval shape. In all species of the Psyllidae, a trochantin convexity is observed at the ventral side of the thorax, before the mesocoxa. An incision in the middle of the anterior margin of the mesosternum is also observed. In comparison to the mesoscutellum, the metascutellum is half its width and it is shorter if measured in the mid-line. In the species of this family, the trochantin at the metathorax is tuberculated and the meracanthus is distinct and horn-shaped. Five probably monophyletic subfamilies have been distinguished within the Psyllidae (i.e. Macrocorsinae, Psyllinae, Acizzinae, Aphalarodinae, Ciriacreminae), but the relations between them remain unknown (Burckhardt, Ouvrard 2012). The conducted cladistic analysis of the thorax and its appendages groups the species of the Psyllidae family (clade M, Fig. 73) in concordance with the division of subfamilies proposed by Burckhardt and Ouvrard (2012).

The Triozidae is well diagnosed (Hollis 1984, Burckhardt 1988, Burckhardt, Lauterer 1997b) and probably monophyletic. No subfamilies have been distinguished within Triozidae (Burckhardt, Ouvrard 2012). The definitions of many genera within that family are unclear and artificial, and the phylogenetic relations between them remain unknown (Burckhardt, Ouvrard 2012). The presented research confirms the monophyly of the Triozidae in which the species are characterized by a U-shaped anterior margin of the pronotum and well-developed cavities at the sides of the pronotum which separate its central and lateral parts. The letaral portions are extended in the direction of the head. Additionally, in all the species of that family, the anal break at the forewings is distant from the apex of the vein Cu_{1b}. None of these characters were found in any other families so far. Except for the characters specified above, the species of the Triozidae family exhibit a head strongly inclined downwards (45–90°), while the dorsal margin of the thorax is slightly arched in the side-view. The pronotum of the Triozidae is distinctly narrower than the head with eyes and its posterior margin is slightly arched and free of incisions. Other characters of the pronotum are its vertical or near-vertical situation, the fact that it is often fully or partially covered by the head as well as the length of the pronotum varying between the central and lateral portions. The prothoracic pleurites in the Triozidae are characterized by comparable sizes, anteroventral displacement and the fact that the separating sulcus reaches the posterior angle of the pronotum. The three additional sclerites between the prothorax and the mesothorax are visible in that group of species. The mesothorax in that family is relatively narrow – the mesopraescutum is narrower than the pronotum and over three times the length of pronotum measured in the central line. The anterior margin of the mesoscutellum is always U-shaped. The width of the mesoscutum of the Triozidae is over twice its length. When measured in the central line, its length is similar to the length of the mesopraescutum or slightly longer, but its width is over 1.5 times the width of the mesopraescutum. The mesoscutellum in Triozidae is U-shaped and over 2.5 times narrower than the mesoscutum. Its posterior margin is straight and free of incisions. The mesothorax of these species includes a short (and) or indistinct, diagonal, mesopleural sulcus as well as a distinct, diagonal and (or) short anapleural cleft. The courses of these structures do not intersect. All of the Triozidae species exhibit an oval parapteron that is larger than the tegula, which is also an oval structure in all the species. The ventral side of the thorax in Triozidae is characterized by a distinct convexity of the trochantin in front of the mesocoxa and an incision in the anterior margin of the mesosternum. Apart from the above, other characters include a well-visible pleurosternal sulcus, a triangular

basisternum and lateral parts of the kapisternum that are narrower than the width of the head with eyes. The lateral parts of the kapisternum are extended by small oval structures. The metascutum of the Triozidae species is well visible from the dorsal side and the trapezoidal metascutellum is of the same width as the mesoscutellum, but shorter when measured in the mid-line line. The pleural sulcus at the metathorax was not preserved, while the tuberculated trochantin and horn-shaped meracanthus are present.

To conclude, the conducted analysis of the morphology of thorax and its appendages indicated that among eight of the families currently distinguished by Burckhardt and Ouvrard (2012), five may be considered monophyletic. These are: Carsidaridae, Homotomidae, Phacopteronidae, Psyllidae and Triozidae. The remaining three families: Aphalaridae, Calophyidae and Liviidae, are regarded as polyphyletic. When grouping the species in the families referred to earlier, Burckhardt and Ouvrard (2012) have noted the lack of data regarding the phylogenetic relations within these families. The authors have also pointed to the probable monophyly of subfamilies which constitute the families, but these have not been yet confirmed by analyses.

The previous attempts to create a classification in which the species of the families Aphalaridae, Calophyidae and Liviidae would constitute monophyletic groups have not been successful. The species included in the Aphalaridae *sensu* Becker-Migdisova (1973), White and Hodkinson (1985), Li (2011) or Burckhardt and Ouvrard (2012), did not constitute a monophyletic group. The Calophyidae *sensu* White and Hodkinson (1985), Li (2011) and Burckhardt and Ouvrard (2012), as well as the Liviidae *sensu* White and Hodkinson (1985), Li (2011) and Burckhardt and Ouvrard (2012), also are not monophyletic.

The presented research regarding the morphology of the thorax and its appendages have not indicated synapomomorphies that would allow for the transfer of individual taxa of the three families so as they would form monophyletic groups. Due to the above, the author does not propose the reclassification or liquidation of taxa earlier established by Burckhardt and Ouvrard (2012), although from the cladistic point of view there are no phylogeny grounds to maintain such a classification.

5 Conclusion

1. The work includes the description and documentation of thorax morphology in the representatives of all higher taxonomic units within the superfamily Psylloidea. Within the work, the morphological characteristics of that body section have also been provided for the insects of the extinct family Liadopsyllidae, which is recognized as the ancestral family of extant psyllids, as well as for the superfamily Aleyrodoidea – considered as their sister group within the Sternorrhyncha suborder. Both groups have been applied as outgroups.
2. Based on cladistic analysis methods, all the characters of the thorax have been polarized in relation to external groups.
3. New data regarding the morphology of the thorax and its appendages have been embedded in a matrix. Part of the characters relating to the morphology of thorax appendages has been derived from the literature.
4. The determination of phylogenetic relations based on the morphology of thorax and its appendages has been conducted by means of cladistic analysis software.
5. The relations between the analyzed taxa have been presented in cladograms.
6. Phylogenetic relations between the taxa of psyllids have been reviewed based on the analysis of the thorax including the appendages in comparison with other proposals of this group's phylogeny.
7. The characteristics of families and subfamilies have been complemented with new characters identified within the thorax. Based on the above, a key has been created for the identification of species from the individual subfamilies of the World fauna of psyllids.

6 Key for the determination of subfamilies of psyllids using the morphological characters of the thorax with the appendages

1. Veins Rs and M_{1+2} on forewing in contact forming cross; costal break in distance of vein R_1; costal margin not curved .... Phacopteronidae
–. Veins Rs and M_{1+2} on forewing parallel, not in contact, costal break near vein R_1, costal margin curved 2
2. Crossvein between veins Rs and M present on forewing; dorsal margin of thorax almost straight ..... Carsidaridae
–. Crossvein between veins Rs and M on forewing absent; dorsal margin of thorax weakly or strongly arched 3
3. Cu_1 stem on forewing absent or very short; Cu of hindwing unbranched 4
–. Cu_1 stem on forewing present, long; Cu of hindwing branched 6
4. Ratio F/G (Fig. 4) on mesoscutum is 2; parapteron not oval; metatarsal spurs absent .... Dynopsyllinae, Homotomidae
–. Ratio F/G (Fig. 4) on mesoscutum is 1.5; parapteron oval; metatarsal spurs present 5
5. Anapleural cleft distinct, almost horizontal and long; mesopraescutum narrower than pronotum; metascutellum trapezoidal .... Homotominae, Homotomidae
–. Anapleural cleft distinct, oblique and (or) short, mesopraescutum as wide as pronotum; metascutellum rectangular .... Macrohomotominae, Homotomidae
6. Pronotum distinctly narrower than head with compound eyes; lateral part of katepisternum in ventral side narrower than width of head with eyes; trochantin on metathorax tuberculated 7
–. Pronotum as wide as head with compound eyes or slightly narrower; lateral part of katepisternum in ventral side as wide as width of head with eyes or wider; trochantin on metathorax not tuberculated 12
7. Anterior margin of pronotum and mesoscutum u-shaped; in dorsal view, lateral part of pronotum separated by well-developed incision, lateral part protruding anteriad; propleurites displaced ventrally; mesoscutellum narrow, trapezoidal ..... Triozidae
–. Anterior margin of pronotum and mesoscutum arched; in dorsal view, lateral part of pronotum separated by well-developed incision, lateral part not protruding anteriad; propleurites displaced antero-ventrally; mesoscutellum broad, trapezoidal 8
8. Posterior margin of pronotum slightly arched, with incision; mesopraescutum indistinctly separated from mesoscutum .... Aphalaroidinae, Psyllidae
–. Posterior margin of pronotum slightly arched, without incision; mesopraescutum distinctly separated from mesoscutum 9
9. Pleural sulcus is connected with anapleural cleft ..... Ciriacreminae, Psyllidae
–. Pleural sulcus is not connected to anapleural cleft 10
10. Posterior margin of mesoscutellum with incision in the middle; anapleural cleft distinct, oblique and (or) short .... Psyllinae, Psyllidae

–. Posterior margin of mesoscutellum straight, without incision; anapleural cleft distinct, almost horizontal and long 11

11. Metascutum visible in dorsal view; metascutellum rectangular; proepisternum and proepimeron not subequal; mesopleural sulcus almost horizontal; basisternum triangular ..... Acizziinae, Psyllidae

–. Metascutum not visible in dorsal view; metascutellum trapezoidal; proepisternum and proepimeron the same size; mesopleural sulcus long, distinct and oblique; basisternum oval ..... Macrocorsinae, Psyllidae

12. Vein M_{1+2} curved backwards 13

–. Vein M_{1+2} curved forwards 16

13. Meracanthus absent or very small tubelcular 14

–. Meracanthus present horn-shaped 17

14. Ratio F/G (Fig. 4) on mesoscutum is 1 ..... Togepsyllinae, Aphalaridae

–. ratio F/G on mesoscutum is about 1.5 15

15. Transepimeral sulcus hardly visible; metatibia with an open crown of strongly sclerotized apical spurs ..... Rhinocolinae, Aphalaridae

–. Metatibia with an grouped apical spurs; transepimeral sulcus well developed ..... Spondyliaspidinae, Aphalaridae

16. Propleurites broad, lateral; mesopraescutum along less than 3 times as long as pronotum; mesopraescutum distinctly separated from mesoscutum; metapostnotum without any tubercles; cell m_1 of forewing narrow ..... Aphalarinae, Aphalaridae

–. Propleurites displaced antero-ventrally; mesopraescutum more than 3 times longer than pronotum along mid line; mesopraescutum indistinctly separated from mesoscutum; pair of tubercles present of metapostnotum; cell m_1 wide ..... Pachypsyllinae, Aphalaridae

17. Pronotum longer or shorter along the mid line than along lateral portions; cell m_1 the same size as cell cu_1 ..... Liviinae, Liviidae

–. Pronotum along mid line as long as along lateral portions; cell m_1 not the same size as cell cu_1 18

18. Propleurites displaced antero-ventrally ..... Euphyllurinae, Liviidae

–. Propleurites not displaced antero-ventrally 19

19. Parapteron and tegula the same size; metascutellum as long as mesoscutellum in mid line; metatarsal spurs absent ..... Calophyinae, Calophyidae

–. Parapteron bigger than tegula; metascutellum shorter than mesoscutellum in mid line; metatarsal spurs present ..... Mastigimatinae, Calophyidae

References

Audouin V. 1824: Recherches anatomiques sur le thorax des animaux articule's et celui des insectes hexapodes en particulier. *Annales des Scientes Naturelles*, 1: 97–135.

Becker-Migdisova E.E. 1973: Sistema psillomorf (Psyllomorpha) i polozheriie gruppy v otryade ravnokrylykh (Homoptera) [On the systematics of the Psyllomorpha and the position of the group within the order Homoptera]. In: E.P. Narchuk (Ed), *Doklady na dvadzat chetvertom escheghodnom chtenii pamyati N.A. Kholodovskogo.* Nauka, Leningrad, p. 90–118.

Becker-Migdisova E.E. 1985: Iskopaemye nasekomye Psillomorfy [Fossil Psyllomorpha]. *Trudy Paleontologičeskogo instituta*, 206: 1–94.

Becker-Migdisova, E.E., Aizenberg, E.E. 1962: Infraotryad Aphidomorpha. [Infraorder Aphidomorpha]. 194–199. In: Rohdendorf, B.B. (Ed.), *Osnovy palontologii. Chlenistonogie. Trakheïnye i Khelicerovye.* [Fundamentals of Palaeontology. Arthropoda. Tracheata and Chelicerata.] **9**. Izdatel'stvo Akademii Nauk SSSR, Moscow. Published in English as: Becker-Migdisova, E.E., Aizenberg, E.E. 1991. Infraorder Aphidomorpha. In: Rohdendorf, B.B. (Ed.), Fundamentals of Paleontology. Arthropoda. Tracheata and Chelicerata **9**. 218–289. General Editor English Translation: Davis, D.R. Smithsonian Institution Libraries and The National Science Foundation, Washington D.C. p. 1–894.

Bhanotar R.K., Ghosh M., Ghosh L.K. 1971: A new tribe of Psyllidae (Homoptera) from India. *Bulletin of Entomology, Entomological Society of India*, 12: 109–112.

Boselli F.B. 1928: Studii sugli Psyllidi. (Homoptera: Psyllidae Chermidae). I–II. I. Contributo alla conoscenza della psylla delfico (*Homotoma ficus* L.). II. Descrizione di una nuova specie di *Paurocephala* della cina e dei suoi stadii larvali. *Bolletino del Laboratorio di Zoologia Generale e Agraria del R. Istituto Superiore Agrario, Portici* 21: 218–264.

Brittain W.H. 1922: The morphology and synonymy of *Psyllia mali* Schmidberger. *Proceedings of the Acadian Entomological Society*, 8: 23–51.

Brown R.G., Hodkinson I.D. 1988: Taxonomy and ecology of the jumping plant-lice of Panama (Homoptera: Psylloidea). *Entomonograph*, 9: 1–304.

Burckhardt D. 1986: A new *Russelliana* species (Homoptera: Psyllidae) on *Adesmia* (Leguminosae). *Revista Chilena de Entomologia*, 14: 95–97.

Burckhardt D. 1987a: Jumping plant lice (Homoptera: Psylloidea) of the temperate Neotropical region. Part 1: Psyllidae (subfamilies Aphalarinae, Rhinocolinae and Aphalaroidinae). *Zoological Journal of the Linnean Society*, 89: 299–392.

Burckhardt D. 1987b: Jumping plant lice (Homoptera: Psylloidea) of the temperate Neotropical region. Part 2: Psyllidae (subfamilies Diaphorininae, Acizziinae, Ciriacreminae and Psyllinae). *Zoological Journal of the Linnean Society*, 90: 145–205.

Burckhardt D. 1988: Jumping plant lice (Homoptera: Psylloidea) of the temperate Neotropical region. Part 3: Calophyidae and Triozidae. *Zoological Journal of the Linnean Society*, 92: 115–191.

Burckhardt D. 1991: *Boreioglycaspis* and spondyliaspidine classification (Homoptera: Psylloidea). *Raffles Bulletin of Zoology*, 39: 15–52.

Burckhardt D. 2005: *Ehrendorferiana*, a new genus of Neotropical jumping plant lice (Insecta: Hemiptera: Psylloidea) associated with conifers (Cupressaceae). *Organisms Diversity and Evolution*, 5: 317–319.

Burckhardt D. 2008: Jumping plant-lice (Hemiptera, Psylloidea) associated with Diostea (Verbenaceae). *Deutsche Entomologische Zeitschrift*, 55(1): 79–89 / doi 10.1002/mmnd.200800005.

Burckhardt D., Basset Y. 2000: The jumping plant-lice (Hemiptera, Psylloidea) associated with Schinus (Anacardiaceae): systematics, biogeography and host plant relationships. *Journal of Natural History*, 34: 57–155.

Burckhardt D., Lauterer P. 1989: Systematics and biology of the Rhinocolinae (Homoptera: Psylloidea). *Journal of Natural History*, 23: 643–712.

Burckhardt D., Lauterer P. 1997a: Systematics and biology of the *Aphalara exilis* (Weber and Mohr) species assemblage (Hemiptera: Psyllidae). *Entomologica scandinavica*, 28: 271–305.

Burckhardt D., Lauterer P. 1997b: A taxonomic reassessment of the triozid genus *Bactericera* (Hemiptera: Psylloidea). *Journal of Natural History*, 31: 99–153.

Burckhardt D., Mifsud, D. 2003: Jumping plant-lice of the Paurocephalinae (Insecta, Hemiptera, Psylloidea): systematics and phylogeny. *Contributions to Natural History (Bern)*, 2: 3–34.

Burckhardt D., Ouvrard D. 2006: The taxonomy, biogeography and host plant relationships of jumping plant-lice (Hemiptera: Psyllidae) associated with creosote bushes (Larrea spp., Zygophyllaceae). *Systematic Entomology*, 32(1): 136–155. doi: 10.1111/j.1365-3113.2006.00352.x

Burckhardt D., Ouvrard D. 2012: A revised classification of the jumping plant-lice (Hemiptera: Psylloidea). *Zootaxa*, 3509: 1–34.

Burckhardt D., Queiroz D. 2013: Phylogenetic relationships within the subfamily Aphalarinae including a revision of *Limataphalara* (Hemiptera: Psylloidea: Aphalaridae) *Acta Musei Moraviae, Scientiae biologicae* (Brno) 98(2): 35–56.

Clark L.R. 1962: The general biology of *Cardiaspina albitextura* (Psyllidae) and its abundance in relation to weather and parasitism. *Australian Journal of Zoology*, 10: 537–586.

Crampton G.C. 1914a: Notes on the thoracic sclerites of winged insects. *Entomological News*, 25: 15–25.

Crampton G.C. 1914b: The ground-plan of a typical thoracic segment in winged insects. *Zoologischer Anzeiger*, 44: 56–67.

Crampton G.C. 1914c: On the misuse of the terms parapteron, hypopteron, tegula, squamala, patagium and scapula. *Journal of the New York Entomological Society*, 22: 248–261.

Crawford D.L. 1914: A monograph of the jumping plant-lice or Psyllidae of the new world. *Bulletin of the United States National Museum*, 85: 1–186.

Drohojowska J. 2009a: General information on thorax morphology of selected species of psyllids (Hemiptera, Psylloidea). *Monograph Aphids and Other Hemipterous Insects*, 15: 5–16.

Drohojowska J. 2009b: Structure of head and thorax of *Livia juncorum* (Latreille, 1978) (Hemiptera, Psylloidea). *Monograph Aphids and Other Hemipterous Insects*, 15: 17–30.

Drohojowska J. 2011: *Eogyropsylla sedzimiri* sp. nov. from Eocene Baltic amber with a key to the species of the fossil genus *Eogyropsylla* Klimaszewski, 1993 (Hemiptera: Sternorrhyncha: Psylloidea). *Zootaxa*, 2803: 41–48.

Drohojowska J., Kalandyk-Kołodziejczyk M., Simon E. 2013: Thorax morphology of selected species of genus *Cacopsylla* Ossiannilsson 1970 (Hemiptera, Psylloidea). ZooKeys, 319: 27–35. doi: 10.3897/zookeys.319.4218.

Drohojowska J., Szwedo J. 2011a: A new whitefly from Lower Crataceous Lebanese amber (Hemiptera: Sternorrhyncha: Aleyrodidae). *Insect Systematic and Evolution*, 42(2): 179–196. doi:10.1163/187631211X568470.

Drohojowska J., Szwedo J. 2011b: New Aleyrodidae (Hemiptera: Sternorrhyncha: Aleyrodomorpha) from the Eocene Baltic amber. *Polish Journal of Entomology*, 80(4): 659–677. doi:10.2478/v10200-011-0051-y.

Drohojowska J., Szwedo J. 2013a: Whiteflies (Hemiptera: Sternorrhyncha: Aleyrodidae) from the Lowermost Eocene Oise amber. *Zootaxa*, 3636(2): 319–347. doi: 10.11646/zootaxa.3636.2.5.

Drohojowska J., Szwedo J. 2013b: *Gapenus rhinariatus* gen.sp.n. from the Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Aleyrodidae). In: Azar D., Engel M.S., Jarzembowski E., Krogmann L., Nel A. and Santiago-Blay J. (Eds.) Insect Evolution in an Amberiferous and Stone Alphabet. Brill, Leiden–Boston, p. 99–110.

Drohojowska J., Szwedo J. 2015: Early Crataceous Aleyrodidae (Hemiptera: Sternorrhyncha) from the Lebanese amber. *Crataceous Research*, 52: 368–389. doi: 10.1016/j.cretres.2014.03.015.

Enderlein G. 1910: 12. Hemiptera. 8. Psyllidae. In: Y. Sjöstedt (Ed.), *Wissenschaftlische Ergebnisse der Schwedischen Zoologischen Expedition nach dem Kilimandjaro, dem Meru und den Umgebenden*

Massaisteppen Deutsch0 Ostafrikas 1905–1906. Tryckt Hos, Stockholm (Sweden), p. 137–144.

Forero D. 2008: The systematics of the Hemiptera. *Revista Columbiana de Entomologia*, 34(1): 1–21.

Grimaldi D.A. 2003: First amber fossils of the extinct family Protopsyllidiidae, and their phylogenetic significance among Hemiptera. *Insect Systematics and Evolution*, 34: 329–344.

Grimaldi D., Engel M.S. 2005: *Evolution of the Insects*. Cambridge University Press, Cambridge.

Gullan P.J., Martin J.H. 2003: Sternorrhyncha (Psylloids, Whiteflies, Aphids and Scale Insects). In: Cardé R.T., Resh V.H. (Eds.), *Encyclopedia of Insects*. Academic Press, Amsterdam, The Netherlands, p. 1079–1089.

Harbach R.E., Greenwalt D. 2012: Two Eocene species of *Culiseta* (Diptera: Culicidae) from the Kishenehn Formation in Montana. *Zootaxa*, 3530: 25–34.

Hennig W. 1981: *Insect Phylogeny*. (Translated and edited by A.C. Pont). J. Wiley and Sons. Chichester, New York, U.S.A, p. 1–514.

Heslop-Harrison G. 1951: The Arytainini of the subfamily Psyllinae, Hemiptera—Homoptera Family Psyllidae. *Annals and Magazine of Natural History*, 12: 417–462.

Heslop-Harrison G. 1952: The number and distribution of the spiracles of the adult psyllid. *Annals and Magazine of Natural History*, 12: 248–260.

Heslop-Harrison G. 1958: Subfamily separation in the Homopterous Psyllidae- III (a-c). *Annals and Magazine of Natural History*, 13: 561–579.

Hodkinson I.D., White I.M. 1979: Homoptera Psylloidea. *Handb Ident Br Insects*, 2: 1–98.

Hollis D. 1973: African gall bugs of the genus *Phytolyma* (Hemiptera, Psylloidea). *Bulletin of Entomological Research*, 63: 143–154.

Hollis D. 1976: Jumping plant lice of the tribe Ciriacremini (Homoptera: Psylloidea) in the Ethiopian region. *Bulletin of the British Museum (Natural History) Entomology series*, 34: 3–83.

Hollis D. 1984: Afrotropical jumping plant lice of the family Triozidae (Homoptera: Psylloidea). *Bulletin of the British Museum (Natural History) Entomology*, 49: 1–102.

Hollis D. 1987: A review of the Malvales-feeding psyllid family Carsidaridae (Homoptera). *Bulletin of the British Museum (Natural History) Entomology series*, 56: 87–127.

Hollis D., Broomfield P.S. 1989: Ficus-feeding psyllids (Homoptera), with special reference to the Homotomidae. *Bulletin of the British Museum (Natural History) Entomology series*, 58: 131–183.

Hollis D., Martin J.H. 1997: Jumping plant-lice (Insecta: Hemiptera) attacking *Lonchocarpus* species (Leguminosae), including 'Black Cabaga Bark', in Belize. *Journal of Natural History*, 31: 237–267.

Journet A.R.P., Vickery V.R. 1978: Studies on Nearctic *Craspedolepta* Enderlein, 1921 (Homoptera: Psylloidea): external morphology. *Canadian Entomologist*, 110: 13–36.

Klimaszewski S.M. 1964: Studia nad układem systematycznym podrzędu Psyllodea. *Annales Zoologici*, 22(5): 81–138.

Klimaszewski S.M. 1975: *Psylloidea. Koliszki (Insecta: Homoptera)*. Fauna Polski, 3, p. 1–295.

Klimaszewski S.M. 1979: Studies on systematic of the suborder Psyllodea, *U.S. Department of Agriculture and the National Science*, 1–56.

Klimaszewski S.M. 1993a: New species of Eocene psyllids representing the tribe Palaeopsylloidini Becker-Migdisova (Homoptera, Psylloidea). *Acta Biologica Silesiana*, 22: 9–18.

Klimaszewski S.M. 1993b: The structure of hind wings in Psyllodea (Homoptera) and its possible significance in recognizing the relationships within this suborder. *Acta Biologica Silesiana*, 22: 57–68.

Klimaszewski S.M. 1993c. New species of Miocene psyllids (Homoptera, Psylloidea). Prace naukowe Uniwersytetu Śląskiego. *Acta Biologica Silesiana*, Katowice 22(39): 19–29.

Klimaszewski S.M. 1995: *Succinopsylla dominicana* n. gen. n. sp., a new jumping plant louse from the Dominican amber (Insecta: Homoptera, Rhinopsyllidae). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 78: 189–195.

Klimaszewski S.M. 1996: New psyllids (Homoptera, Psylloidea) from Dominican amber. *Acta Biologica Silesiana*, 29: 24–44.

Klimaszewski S.M. 1997a: New data on the jumping plant-lice: I–III (Homoptera, Psylloidea). *Acta Biologica Silesiana*, 29: 56–65.

Klimaszewski S.M. 1997b: New psyllids (Homoptera, Psylloidea) from Dominican amber. *Acta Biologica Silesiana*, 29: 24–44.

Klimaszewski S.M. 1997c: New psyllids from the Baltic amber (Insecta: Homoptera, Aphalaridae). *Mitteilungen aus dem Geologisch-Palaeontologischen Institut der Universitaet Hamburg*, 80: 157–171.

Klimaszewski S.M. 1997d: Further data concerning Dominican amber jumping plant lice (Homoptera, Psylloidea). *Acta Biologica Silesiana*, 32: 19–27.

Klimaszewski S.M. 2001: Jumping plant lice from the family Aphalaridae in Central Asian Province (Hemiptera: Sternorrhyncha: Psylloidea). *Annals of the Upper Silesian Museum in Bytom Entomology*, 10–11: 179–201.

Klimaszewski S.M., Wojciechowski W. 1992: Relationships of recent and fossil groups of Sternorrhyncha as indicated by the structure of their forewings. Wydawnictwo Uniwersytetu Śląskiego, Katowice, 1318, p. 1–50.

Kwon Y.J. 1983: *Psylloidea of Korea* (Insecta Koreana Series 2). Editorial committee of Insecta Koreana, Seoul, p. 1–181.

Latreille P.A. 1807: *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata* (Tomus tertius). A. Koenig, Paris, p. 1–280.

Li F. 2002: Homoptera: Psylloidea. In: F.-s. Huang, H. Yin, R. Zeng, M. Lin and M. Gu (Eds.), *Forest insects of Hainan.* Science Press, 1064pp., Beijing, p. 171–189.

Li F. 2011: *Psyllidomorpha of China* (*Insecta: Hemiptera*). Science Press, Beijing, China, i–xli, p. 1–1976.

Loginova M.M. 1964: Podotrjad Psyllinea. In: G.Y. Bei-Bienko (Ed.), *Opredelitel' nasekomykh Evropeiskoi chasti SSSR*. Izdatel'stvo „Nauka", Moscow, Russia, p. 437–482.

Löw F. 1879: Zur Systematic der Psylloden. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien, 28: 586–610.

Martin J.H. 2007: Giant whiteflies (Sternorrhyncha, Aleyrodidae): a discussion of their taxonomic and evolutionary significance, with the description of a new species of *Udamoselis* Enderlein from Ecuador. *Tijdschrift voor Entomologie*, 150: 13–29.

Matsuda R. 1970: Morphology and evolution of the insect thorax. *Memoirs of the Entomological Society of Canada*, 76: 1–431.

Matsuda R. 1979: Morphologie du thorax et des appendices thoraciques des insectes. In: Grasse' P-P. (Ed) Traite' de zoologie. Tome VIII, Fascicule II. Paris: Masson, p. 1–289.

Minkiewicz S. 1924: The apple sucker *Psylla mali* Schmidberger. I. Morphology. Bulletin of the Polish Academy of Sciences, *Cl Sci Math Nat, Ser B: Sci Nat*, 589–603.

Olivares T.S., Burckhardt D. 1997: Jumping plant-lice of the New World genus Calinda (Hemiptera: Psylloidea: Triozidae). *Revue Suisse de Zoologie*, 104(2): 231–344.

Ossiannilsson F. 1992: The Psylloidea (Homoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, 26: 1–347.

Ouvrard D. 2002: Phylogenetic systematics of Hemiptera Psylloidea: comparative morphology of the thorax and secondary structures of the 18S rRNA. *Bulletin de la Société Zoologique de France*, 127: 345–357.

Ouvrard D., Bourgoin T., Campbell B. 2002: Comparative morphological assessment of the psyllid pleuron (Insecta, Hemiptera, Sternorrhyncha). *Journal of Morphology,* 252: 276–290.

Ouvrard D., Burckhardt D., Greenwalt D. 2013: The oldest jumping plant-louse (Hemiptera: Sternorrhyncha) with comments on the classification and nomenclature of the Palaeogene Psylloidea. *Acta Musei Moraviae, Scientiae biologicae* (Brno), 98(2): 21–33.

Ouvrard D., Burckhardt D., Azar D., Grimaldi D. 2010: Non-jumping plant-lice in Cretaceous amber (Hemiptera: Sternorrhyncha: Psylloidea). *Systematic Entomology*, 35: 172–180.

Ouvrard D., Burckhardt D., Soulier-Perkins A., Bourgoin T. 2008: Comparative morphological assessment and phylogenetic significance of the wing base articulation in Psylloidea (Insecta, Hemiptera, Sternorrhyncha). *Zoomorphology*, 127: 37–47.

Percy D.M. 2003: Radiation, diversity, and host-plant interactions among island and continental legume-feeding psyllids. *Evolution*, 57: 2540–2556.

Pflugfelder O. 1941: Psyllina. In: Bronns H.G., (Ed.) *Klassen und Ordnungen des Tierreichs*. Fünfter Band: Arthropoda. 3. Abteilung: Insecta. VIII. Buch, Teil b. Leipzig: Akademische Verlagsgesellschaft Becker and Erler Kom.-Ges.

Popov Yu. A. 1980: Hemipteroidea. In: Rohdendorf B.B, Rasnitsyn A.P., (Eds.), *Historical development of the class Insecta. Trudy Paleontologicheskogo Instituta AN SSSR*, 178, p. 58–69 [in Russian).

Popov, Yu. A. 1981: Historical development and some questions on the general classification of Hemiptera. *Rostria* (Suppl.), 33: 85–99.

Quaintance A.L., Baker A.C. 1913: Classification of the Aleyrodidae. *U.S. Department of Agriculture, Bureau of Entomology (Technical Series)* 27: 1–93.

Ramirez-Gomez C. 1955: Los psilidos de Espana. *Boletin de la Real Sociedad Espanola de Historia Natural* (Biol), 53: 151–217.

Schlee D. 1969a: Sperma-übertragung in ihrer Bedeutung für das phylogenetische System der Sternorrhyncha. Phylogenetische Studien an Hemiptera. I. Psylliformes Psyllina und Aleyrodina) als monophyletische Gruppe. *Zeitschrift für Morphologie der Tiere*, 64: 95–138.

Schlee D.1969b: Die Verwantschaftsbeziehungen innerhalb der Sternorrhyncha auf Grund synapomorphe Merkmale. Phylogenetische Studien an Hemiptera. II. Aphidiformes (Aphidina–Coccina) als monophyletische Gruppe. *Stuttgarter Beiträge zur Naturkunde*, 199: 1–19.

Schlee D.1969c: Bau und Funktion des Aedeagus bei Psyllina und deren Bedeutung für systematische und phylogenetische Untersuchungen (Insecta, Hemiptera). Phylogenetische Studien an Hemiptera. III. Entkräftung eines argument gegen die Monophylie der Sternorrhyncha. *Zeitschrift für Morphologie der Tiere*, 64: 139–150.

Schwarz E.A. 1898: Notes on the lerp insects (Psyllidae) of Australia. *Proceedings of the Entomological Society of Washington*, 4: 66–75.

Shcherbakov D.E. 1983. Early evolution of the Auchenorrhyncha. M. S. thesis. Paleontological Institut AN SSSR. Moscow [in Russian].

Shcherbakov D.E. 1988: New Mesozoic Homoptera. *Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya Trudy* [*Transactions of the Joint Soviet-Mongolian Paleontological Expedition*], 33: 60–63 [in Russian].

Shcherbakov D.E. 1990: Extinct four–winged ancestors of scale insects (Homoptera: Sternorrhyncha). *Proceedings of the Sixth International Symposium of Scale Insect Studies*, part II, Cracow, August 6–12, 1990. Agricultural University Press, Kraków, p. 23–29.

Shcherbakov D.E. 2000: Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal*, 34: 251–267

Shcherbakov D.E. 2005: Fossils versus molecules and cladistics: controversies over the Hemiptera phylogeny. *12th International Auchenorrhyncha Congress*, Berkeley, 7–12 August 2005. I-1–I-3.

Shcherbakov D.E. 2007: Extinct four-winged precoccids and the ancestry of scale insects and aphids (Hemiptera). *Russian Entomological Journal*, 16: 47–62.

Shcherbakov D.E., Popov Yu.A. 2002: 2.2.1.2.5. Superorder Cimicidea Laicharting, 1781 Order Hemiptera Linné, 1758. The Bugs, Cicadas, Plantlice, Scale Insects, etc. (= Cimicida Laicharting, 1781, = Homoptera Leach, 1815 + Heteroptera Latreille, 1810) In*:* Rasnitsyn, A.P., Quicke, D.L.J. (Eds.). *History of Insects*. Kluwer Academic Publishers, Dordrecht / Boston / London, 143–157.

Snodgrass R.E. 1908: A comparative study of the thorax in Orthoptera, Euplexoptera, and Coleoptera. *Proceedings of the Entomological Society of Washington*, 9: 95–108.

Snodgrass R.E. 1909: The thorax of insects and the articulation of the wings. *Proceedings of the United States National Museum*, 36: 511–595.

Snodgrass R.E. 1927: Morphology and mechanism of the insect thorax. *Smithson Misc Collect*, 80: 1–108.

Snodgrass R.E.1935: Principles of insect morphology. New York: McGraw-Hill.

Stough H.B. 1910: The hackberry psylla, *Pachypsylla celtidismammae* Riley. A study in comparative morphology. *Kansas University Science Bulletin*, 5: 121–165.

Taylor L.H. 1918: The thoracic sclerites of Hemiptera and Heteroptera. *Annals of the Entomological Society of America*, 11: 225–254.

Thao M.L., Moran N.A., Abbot P., Brennan E.B., Burckhardt D.H., Baumann P. 2000: Cospeciation of psyllids and their primary prokaryotic endosymbionts. *Applied and Environmental Microbiology*, 66: 2898–2905.

Tremblay E. 1965: Studio morfo-biologico sulla *Trioza tremblayi* Wagner (Hemiptera-Homoptera, Psyllidae). *Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri, Portici*, 23: 37–138.

Tuthill L.D., Taylor K.L. 1955: Australian genera of the family Psyllidae (Hemiptera: Homoptera). *Australian Journal of Zoology*, 3: 227–257.

Vondráček K. 1951: Jumping plant-lice in the collections of the Moravian Museum (Brno). Melichar's collection revised, part I. *Acta Musei Moraviae (Scientae naturales)*, 36: 123–129.

Vondráček K. 1957: *Mery-Psylloidea*. (Fauna CSR, Svazek 9). [*Jumping plant-lice – Psylloidea*. Fauna of Czechoslovakia, Volume 9]. Československá akademie věd, Praha, Czechoslovakia, p. 1–431.

Vondráček K. 1963: Jumping plant-lice (Psylloidea-Homoptera) of Central Africa. Part I (Congo). *Acta Entomologica Musei Nationalis Pragae*, 35: 263–290.

Weber H. 1929: Kopf und Thorax von *Psylla mali* Schmidb.(Hemiptera-Homoptera). *Zeitschrift für Morphologie und Ökologie der Tiere*, 14: 59–165.

Weber H. 1931: Lebensweise und Umweltbeziehungen von *Trialeurodes vaporariorum* (Westwood) (Homoptera- Aleurodina). *Zeitschrift für Morphologie und Ökologie der Tiere*, 23. 1931.

Weber H. 1935: Der Bau der Imago der Aleurodinen. Ein Beitrag zur vergleichenden Morphologie des Insektenkorpers. *Zoologica 89*. E. Schweizerbart'sche Verlagsbuchhandlung (Erwing Nagele). Stuttgart, p. 1–71.

Weber H. 1995: The anatomy of adult Aleyrodids. Translated by: Schulthess F.E. An English translation of *Zoologica*, Heft 89, Stuttgart 1935. Schweizerbart'sche Verlagsbuchhandlung (Erwing Nagele). Stuttgart, 1995.

Wegierek P. 2002: Relationships within Aphidomorpha on the basis of thorax morphology. *Prace Naukowe Uniwersytetu Śląskiego w Katowicach* 2101. Wydawnictwo Uniwersytetu Śląskiego, Katowice, p. 1–106.

Witlaczil E. 1885: Die Anatomie der Psylliden. *Zeitschr. F. wiss. Zool.*, Berlin, 42: 569–638.

List of figures

Jowita Drohojowska

Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)

Streszczenie

Praca zawiera opis i dokumentację budowy tułowia 59. gatunków koliszków, przedstawicieli wszystkich rodzin i podrodzin (za wyjątkiem Atmetocraniinae, Metapsyllinae, Symphorosinae) w obrębie nadrodziny Psylloidea wg klasyfikacji Burckhardt, Ouvrard (2012). Przedstawiono także charakterystykę budowy tego odcinka ciała dla owadów z kopalnej rodziny Liadopsyllidae uważanej za przodków współczesnych koliszków oraz owadów z rodziny Aleyrodoidea, grupy uznanej za siostrzaną w obrębie podrzędu Sternorrhyncha. Obie te grupy zostały wykorzystane jako grupy zewnętrzne. Opierając się na kryterium paleontologicznym, porównaniach wewnątrzgrupowych oraz porównaniach pozagrupowych, przeprowadzono analizę kierunków zmian elementów budowy tułowia i jego przydatków oraz wyznaczono polaryzację cech. Ustalenie filogenetycznych relacji w oparciu o budowę morfologiczną tułowia i jego przydatków wykonano przy pomocy analizy kladystycznej, z wykorzystaniem programu komputerowego TNT 1.1 (Goloboff et al., 2008). Relacje pomiędzy analizowanymi taksonami zostały przedstawione na kladogramach. Omówiono relacje filogenetyczne pomiędzy taksonami koliszków w oparciu o analizę tułowia i jego przydatków w porównaniu z innymi propozycjami filogenezy tej grupy. Potwierdzono monofiletyczność pięciu rodzin: Carsidaridae, Homotomidae, Psyllidae, Phacopteronidae oraz Triozidae. W budowie tułowia i jego przydatków nie znaleziono synapomorfii potwierdzających monofiletyczność rodzin: Aphalaridae, Calophyidae i Liviidae. Uzupełniono charakterystyki rodzin i podrodzin o nowe cechy zidentyfikowane w obrębie tułowia. Na ich podstawie stworzono klucz do oznaczania gatunków z poszczególnych podrodzin światowej fauny koliszków.

Jowita Drohojowska

Die Morphologie des Thoraxes und deren Bedeutung für Festsetzung der stammesgeschichtlichen Verwandtschaft innerhalb der Superfamilie *Psylloidea* (*Hemiptera*, *Sternorrhyncha*)

Zusammenfassung

Die Arbeit beinhaltet die Charakteristik von der Morphologie des Thoraxes und den Nachweis dafür bei 59 Arten der Blattflöhe, Vertretern aller Familien und Unterfamilien (mit Ausnahme von *Atmetocraniinae*, *Metapsylllinae*, *Symphorosinae*) innerhalb der Superfamilie *Psylloidea* nach der Klassifizierung von Burckhardt; Ouvrard (2012). Die Verfasserin präsentiert die Charakteristik von dem Körperteil für Insekte aus der als Vorfahren der heutigen Blattflöhe geltenden fossilen Familie *Liadopsyllidae* und für Insekte aus der innerhalb der Unterordnung *Sternorrhyncha* als eine Schwestergruppe geltenden Familie *Aleyrodoidea*. Die beiden Gruppen dienten als äußere Gruppen. In Anlehnung an paläontologisches Kriterium, an das Gruppeninnere betreffende Vergleiche und Außergruppenvergleiche wurde erforscht, in welcher Richtung sich die einzelnen Elemente von der Morphologie des Thoraxes und dessen Anhänge veränderten und wie sich diese Eigenschaften differenzierten. Stammesgeschichtliche Verwandtschaftsverhältnisse wurden anhand der Morphologie des Thoraxes und dessen Anhänge mittels phylogenetischer Analyse mithilfe des Computerprogramms TNT 1.1 (Goloboff et al., 2008) festgestellt. Die Wechselbeziehungen zwischen den zu untersuchten Taxa wurden an Kladogrammen dargestellt. Phylogenetische Verhältnisse zwischen den Taxa von Blattflöhen wurden anhand der Analyse des Thoraxes und dessen Anhänge untersucht und mit anderen Vorstellungen von der Phylogenese der Gruppe verglichen. Es hat sich bewahrheitet, dass folgende fünf Familien: *Carsidaridae*, *Homotomidae*, *Psyllidae*, *Phacopteronidae* und *Triozidae* monophyletisch sind. In der Morphologie des Thoraxes und dessen Anhänge wurde keine Synapomorphie festgestellt, die eine Monophylogenese von den Familien: *Aphalaridae*, *Calophyidae* und *Liviidae* bestätigen würde. Die Verfasserin vervollständigte außerdem die Charakteristiken von den einzelnen Familien und Unterfamilien mit den im Bereich des Thoraxes neu identifizierten Merkmalen. Auf der Grundlage wurde ein Bestimmungsschlüssel entwickelt, mit dessen Hilfe die aus den einzelnen Unterfamilien stammenden und heutzutage lebenden Arten der Blattflöhe bestimmt werden können.

Copy editing and proofreading Gabriela Marszołek

Cover design Kamil Gorlicki

Technical editing Małgorzata Pleśniar

Typesetting Edward Wilk

ISSN 0208-6336
ISBN 978-83-8012-824-8
(print edition)
ISBN 978-83-8012-825-5
(electronic edition)

Publisher
Wydawnictwo Uniwersytetu Śląskiego
ul. Bankowa 12B, 40-007 Katowice
www.wydawnictwo.us.edu.pl
e-mail: wydawus@us.edu.pl

First impression. Printed sheets: 21.5 + 6 pages (insert)
Publishing sheets: 17.5
Offset paper grade III, 90 g
Price 26 zł (+ VAT)

Printing and binding
EXPOL, P. Rybiński, J. Dąbek, Spółka Jawna
ul. Brzeska 4, 87-800 Włocławek

More about this book

PRICE 26 ZŁ
(+ VAT)

ISSN 0208-6336
ISBN 978-83-8012-824-8